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MEASUREMENTS OF FISH TARGET STRENGTH: A REVIEW

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ABSTRACT

The concept of target strength and its application to the quantitative assessment of fishery resources are discussed. Methods of determining the echo characteristics of fish are reviewed and a number of results presented. Among the more important of these results are: (1) practically every case of interest to the fishing industry is in an acoustic region in which the target strength varies widely with fish size and aspect and acoustic frequency, (2) the major contributors to target strength in this region have been determined to be the swim bladder, flesh, and skeleton, and (3) the average maximum side-aspect and dorsal-aspect target strength of an individual fish have been determined for this region.

Quantitative assessment of fishery resources is a difficult task, and many groups have turned to acoustic techniques to conduct assessment surveys. Present acoustic techniques can give an estimate of the number and dimensions of fish schools in a geographic area and, by estimating the density of the fish in a school, the number of individual fish in the area can be approximated. Measurements of fish target strength are being made by various investigators in an effort to enable the direct acoustic estimation of the number and size of individuals in a school and to enable the direct identification of those individuals by acoustic methods. This paper discusses the concept of target strength and its application to the quantification and/or identification of fish schools, reviews target strength measurement techniques, and discusses some results which have been obtained utilizing these techniques.

TARGET STRENGTH

Active sonars project acoustic energy into the water in an effort to detect objects by the echoes they return, the intensity of the echo depending on the proportion of the sound reflected back to the receiver. The target strength of the echo-producing object is a quantitative measure of its reflecting characteristics and is defined as

$$T = 10 \log \left(\frac{I_1}{I_0} \right), \qquad (1)$$

where I_0 is the intensity of the sound striking the target and I_1 is the intensity of the reflected sound measured at 1 m from the acoustic center of the target. If I_r is the intensity of the reflected sound measured at some distance r from the target, then, assuming that the sound spreads spherically, and there are no losses, I_r will be directly proportional to I_0:

$$I_r = \left(\frac{\sigma}{4\pi} \right) \frac{I_0}{r^2}. \qquad (2)$$

σ is defined as the acoustic cross-section of the target, and $4\pi r^2$ is the spherical surface area through which all the incident energy is reflected. σ depends on the size, shape, and orientation of the target, and, in general, will vary with the angle between the incident direction and the direction of the receiver. In all present fisheries work, this angle is zero and therefore in this paper σ will be the acoustic cross-section of a target for the case in which the source and receiver are located at the same point.

By letting r in equation (2) be equal to 1 m and combining equations (1) and (2),

$$T = 10 \log \left(\frac{\sigma}{4\pi} \right). \qquad (3)$$

Now if I_s is the intensity of the projected sound 1 m from the source,

$$I_0 = \frac{I_s}{r^2} \qquad (4)$$

and therefore,

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$$I_r = \left(\frac{\sigma}{4\pi}\right) \frac{I_s}{r^4}, \qquad (5)$$

or in logarithmic form,

$$10 \log I_r = 10 \log \left(\frac{\sigma}{4\pi}\right) + 10 \log I_s - 40 \log r. \qquad (6)$$

Defining the echo level (E) as 10 log I_r and the source level (S) as 10 log I_s, and rearranging,

$$T = E - S + 40 \log r. \qquad (7)$$

Equation (7) can be used to compute target strength in an ideal medium. In a real medium, however, the actual transmission loss will include effects due to absorption, scattering, refraction, and the boundaries. Hence, in a real medium

$$T = E - S + 2H \qquad (8)$$

where H is the one way transmission loss. H takes into account spreading loss, absorption, and any anomalies. In actual practice H cannot always be reliably predicted and must be measured unless the ranges involved are small. Equation (8) is known as the active sonar equation and is always used in the computation of target strength since it involves only directly measurable quantities—echo level, source level, and transmission loss.

It is impossible for more sound to be reflected from a target than is incident upon it, and it is therefore seemingly impossible for any object to have a positive target strength, yet many large targets do. This is a consequence of the reference distance being 1 m, and the measurements being made at greater distances, with spherical spreading assumed in order to calculate the target strength. However, the spreading loss very close to a target is less than the spherical spreading loss which is assumed, and hence positive target strengths can be obtained for large targets.

The importance of the target strength of a potential target is obvious from the sonar equation (equation (8)). The maximum range at which a target can be detected in any given environment depends on its target strength and the characteristics of the transmitting and receiving systems. Therefore, an estimate of target strength is essential to the effective design and operation of any active sonar system.

The quantification of a fish school, knowing its target strength, is possible because the target strength of a school depends on the average size, number, distribution, and aspect of the individuals in the school. In order to quantify fish schools using target strength information, it is first necessary to determine the size and number of individuals required to produce a given target strength. The initial step in this process is the determination of the target strength of an individual fish. The application of this knowledge to studies on the acoustic interactions of arrays of scatterers will eventually produce accurate predictions of school target strength. The great majority of work done up to this time has been on individual fish, and quite a bit more must be done before this initial step is completed. Definitive work on the quantification and identification of fish schools utilizing target strength information awaits completion of this step.

Reflection of sound from an object in water occurs when the object has an acoustic impedance which differs from that of the water. Acoustic impedance is defined as the product of the density (ρ) of a substance and the velocity of sound (c) in that substance. The proportion of sound reflected from or transmitted into an object in water depends on the magnitude of the impedance mismatch between the object and the water. The simplest case of reflection occurs when a plane wave is normally incident upon a plane boundary between two semi-infinite media. The pressure amplitude reflection coefficient is defined as the ratio of the reflected pressure amplitude to the incident pressure amplitude, and for this case it is found to be $\frac{\rho_2 c_2 - \rho_1 c_1}{\rho_2 c_2 + \rho_1 c_1}$, where $\rho_1 c_1$ is the impedance of the medium in which the incident wave is traveling and $\rho_2 c_2$ is the impedance of the medium upon which the wave is incident. If the second medium is reduced to finite thickness and a third medium is placed behind it (the third medium may or may not be the same as the first), the problem becomes slightly more complicated. When the incident wave arrives at the first boundary, some energy

is reflected and some is transmitted. After this transmitted portion reaches the second boundary, some of the energy is transmitted into the third medium and some is reflected back into the second medium, where it is again partially reflected from the first boundary. This process continues until a steady state is reached. The solution of this problem is relatively easy, but it is interesting because the resultant amplitudes of the transmitted and reflected waves depend on the phases of the component waves. The component waves add vectorially and whether the amplitude of the initially reflected wave is increased or decreased depends on the thickness of the second medium and the wavelength of the incident wave.

The reflection of sound from an infinite plate poorly approximates the reflection from a fish, and it is useful to examine the reflection from a finite object such as a sphere. When the sphere is large compared to the acoustic wavelength, the echo originates from specular reflection, in which the part of the sphere near the point where the sound wave is normally incident produces a coherent reflected wave. When the size of the sphere is comparable to a wavelength, interference effects similar to those mentioned for the plate with finite thickness will cause the acoustic cross-section to vary. When the sphere is small compared to a wavelength, scattering takes place and the acoustic cross-section of a sphere of radius a is proportional to a^6/λ^4 where λ is the wavelength. This solution was obtained by Lord Rayleigh and hence this region is called the region of Rayleigh scattering.

For objects other than spheres, analysis becomes difficult, if not impossible. However, as long as the object is not highly compressible, the concept of the regions of Rayleigh scattering, interference effects, and geometric reflection is valid. For a fish, the distinctions between these regions becomes unclear because of the fish's internal structure. When the fish is very small compared to the acoustic wavelength, Rayleigh scattering can be expected. However, if the fish has a gas-filled swim bladder the gas bubble will resonate at some wavelength in this region, greatly increasing the target strength over that predicted by Rayleigh scattering. When the size of the fish is comparable to the wavelength, interferences will occur among the fish flesh and organs, the skeleton, the gas in the swim bladder, and the boundaries of the fish. When the fish is larger than the wavelength, the dimensions of many of these parts will be comparable to the wavelength and the region of interference effects will be greatly extended into what would be the region of geometric reflection for a homogeneous body.

Cushing et al. (1963) have assumed that the region of interference effects extends from $L/\lambda = 8$ to $L/\lambda = 100$, where L is the fish length, and λ is the acoustic wavelength, and they suggest that for quantitative results this region should be avoided. Neglecting the fact that they have ignored the effects of swim bladder resonance, the limits they have placed on the interference region will now be examined. For a rigid sphere of radius a the limits of the interference region are approximately $1 \leqslant 2\pi a/\lambda \leqslant 10$, and for any other object these limits will probably be farther apart. Measurements on individual fish indicate that interference effects occur at values of $L/\lambda = 0.7$ (Love, 1971) and this can be taken as a lower limit. (This is not to say that it is the lower limit, only that this is as low as measurements have been made.) Haslett (1962a) examined a small number of whiting to determine their "standard dimensions." He found that the diameter of the backbone was about 0.01 the length of the fish. Assuming that the backbone of a fish is the smallest part of a fish which contributes to its echo, this means that if interference effects occur in the backbone until its circumference is something near 10 times as large as the wavelength, as in the case for the sphere, then the upper limit of the interference zone for a fish will be at least $L/\lambda = 200$. Again, measurements have been made which indicate that the upper limit will be at least this high (Haslett, 1969). Therefore, it may be assumed that the limits of the interference region are at least $0.7 \leqslant L/\lambda \leqslant 200$.

If it is assumed that fish of interest to commercial fishermen range from 10 cm to 150 cm, and that fish-finding sonars have frequencies ranging from 10 kHz to 200 kHz, then the range of interest for fisheries applications will be $0.7 \leqslant L/\lambda \leqslant 200$, the limits set for the interference

region. Therefore, although it would be advantageous to avoid the interference region, it is apparent that this is the region in which the work must be done.

METHODS OF TARGET STRENGTH MEASUREMENT

Analytical methods are of limited value in this interference region and experimental methods must be utilized to obtain any valid answers. It is possible to conduct the needed experiments either at sea or in the laboratory, with each type of measurement having its limitations. Whether the measurements are made at sea or in the laboratory, target strength will be determined from the sonar equation, meaning that the source level of the transmitter, the sensitivity of the receiver, and the propagation loss must be known. The calibration of the transmitting and receiving systems is a standard procedure, but propagation loss is much more difficult to determine if long ranges are involved. One way to avoid the propagation loss problem is to make measurements at short ranges, and this is what is done in the laboratory. This, of course, is impossible with large targets. Another method is to use a reference target for which the target strength is known. In this method neither the transmitting nor receiving systems have to be calibrated and the propagation loss does not have to be measured because all echo levels are compared to the reference level. One of the best reference targets is a thin-walled air-filled rubber sphere, although for large targets buoyancy becomes a problem. Another good reference target, which can be used for large targets, is a tri-plane, three mutually perpendicular planes, for which it can be shown that any incident ray will be reflected in a direction exactly opposite to the incident direction. Hence a tri-plane acts as a single plane perpendicular to the incident rays and reflects a large, calculable percentage of the incident energy. It is possible to measure propagation loss directly and this is fairly simple if a transmitting and a receiving ship are utilized. Propagation loss measurements can also be made by placing a calibrated transponder in the vicinity of the target.

Along with the problem of accurately measuring propagation loss, there are other problems associated with target strength measurements at sea, the most critical of these being relative motion between the sonar beam and the fish target. Roll or pitch of the ship can be overcome by using a stabilized sonar beam, but drift can cause the axis of the beam to move off target. Care must also be taken so that the target support structure does not interfere with the measurements. Other problems that can arise are poor weather, high ambient noise levels, and extraneous targets swimming into the beam.

Of course, there are problems associated with laboratory measurements also, the chief one being the limitation on the size of the target. The fish must be placed at a range great enough to insure that the incident sound energy is approximately equal over the complete fish and to insure that the fish is not in the near-field of the transmitter nor the receiver in the near-field of the fish. However, the range must not be so great that reflections from the boundaries or fish support interfere with the measurements. Nevertheless, by judicious choice of measurement range and by using short pulse lengths, unambiguous work can be done in a laboratory tank. In order to obtain a true value of target strength the pulse lengths of the discrete frequency pulses most often utilized by fisheries sonars must be at least twice the length of the target in the direction of propagation, so that an echo can be obtained from all parts of the target simultaneously.

A typical block diagram of the electronics required for target strength measurements is shown in Figure 1. The transmitting system consists of a signal source of known frequency, a means to generate pulses, amplifiers, a transmitting transducer, a system to match the electrical impedances of the amplifier and transducer, and a means to measure the outgoing signal. The receiving system consists of a receiving transducer, amplifiers, a means to gate out unwanted echoes, possibly a filter, and a means to measure the received signal. The electronic system is basically the same whether it is used in the laboratory or at sea.

If all fish were composed of the same homoge-

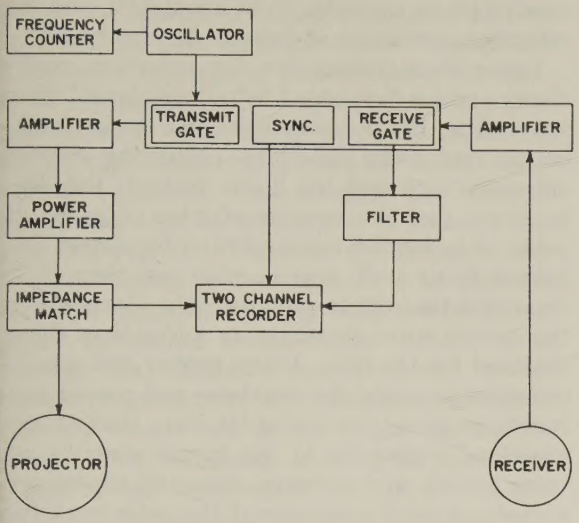

FIGURE 1.—Typical target strength measurement system electronics.

neous material and had the same shape, it would take a comprehensive measurement program to determine the target strength of a fish at all aspects and frequencies because of the complex shape of the body. Since fish are definitely not homogeneous and different species of fish have different shapes and internal structures, the problem of determining the target strengths for all species becomes immense. Considering the differences among individuals of the same species due to age, sex, condition of health, etc., it is obvious that an experimental program to predict completely the target strength of any given fish is impossible. Since the complete determination of the target strength of all fish is impossible, the most that can be hoped for is that experimental techniques will eventually lead to empirical results which can be generalized to apply to any species of importance.

RESULTS OF MEASUREMENTS OF INDIVIDUAL FISH

Most of the early experiments conducted during the 1950's investigated a specific situation. For example, if a researcher had an echo sounder which operated at a given frequency, he would measure the dorsal-aspect target strengths of a number of fish of the commercial species found in his geographic area, in order to obtain an average dorsal-aspect target strength vs. fish size for those species. This information was valuable to anyone designing or using an echo sounder of the same frequency to find these species, but it was of minimal value to anyone else.

A second technique used is just an extension of the earlier technique. With it, different species of fish have been examined at many aspects and/or frequencies in attempts to determine how target strength varies with fish size, species, aspect, and frequency. Figure 2 shows some typical results of this technique. The results are from a live 21-cm black crappie which was rotated about its dorsiventral axis and insonified with frequencies of 30 kHz and 130 kHz. It is seen that the maximum target strength occurs very near the side aspect, where the insonified area is a maximum. At 130 kHz the number of lobes in the pattern is substantially greater, and

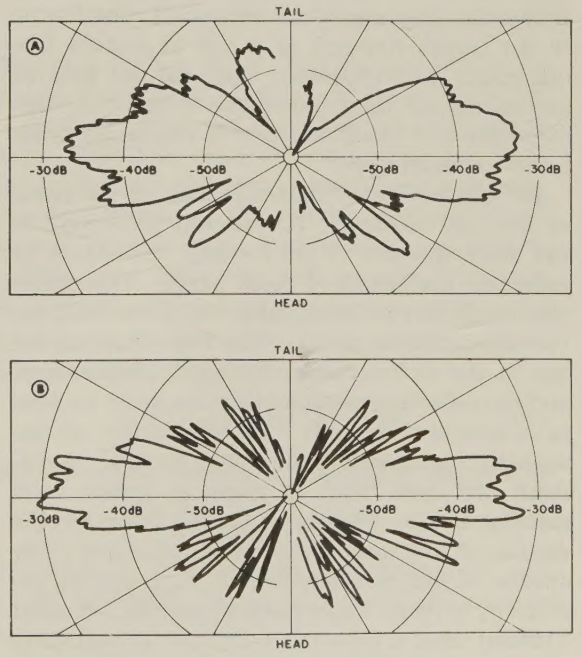

FIGURE 2.—Target strength of a 21-cm black crappie versus aspect. (a) 30 kHz. (b) 130 kHz. (From Love, 1969.)

the maximum target strength slightly greater than at 30 kHz. Although these measurements have produced some useful results on the general changes of target strength with fish size and frequency for aspects of special interest, little has been learned about the fine-scale changes or about the differences among species.

The use of a third technique permits investigation into the nature of the echo-formation process either by dissection or modeling. By dissection, researchers have discovered which parts of a fish are the major acoustic reflectors. By removing the swim bladders from a number of perch, Jones and Pearce (1958) determined that the gas-filled swim bladder accounts for approximately 50% of the dorsal and side-aspect target strengths of perch at $L/\lambda = 4$. Hence, the swim bladder is an important contributor to target strength for L/λ values in the interference region. By systematically removing various parts of a skipjack tuna, Volberg (1963) found that appreciable echoes could be obtained from either the skeleton or a piece of flesh. Diercks and Goldsberry (1970) have indicated the possibility that scales may also be an important contributor to the target strength of a fish at certain frequencies. Unfortunately, they did not remove any scales and their hypothesis is based on considerations of the directivity of the scales as an array of scatterers.

An adjunct to the determination of the parts of the fish which are acoustically important is the determination of the acoustic impedance or reflection coefficient of these parts. The reflection coefficient is defined as it was previously for two semi-infinite media. The impedance of the gas in the swim bladder is readily determined, and the reflection coefficient for the swim bladder is approximately —1. Determination of the acoustic impedance of fish bone or flesh is difficult and care must be taken to insure valid measurements. Shishkova (1958) measured the density of and speed of sound in flesh from a few species of fish and determined the reflection coefficient in fresh water to be about 0.05. Haslett (1962b) used a different technique to indirectly measure the reflection coefficients of flesh and bone from haddock and cod. He found the reflection coefficient of flesh in fresh water to be about 0.05, in seawater to be about 0.02, and the reflection coefficient of bone to be about 0.25.

Using these values for the reflection coefficients and his "standard fish dimensions," Haslett (1962c, 1964) has modeled fish bodies, backbones, and swim bladders. Utilizing rubber ellipsoids to model the fleshy body of the fish, he found that the number of lobes obtained in polar plots for the ellipsoids and for actual fish agreed fairly well, that is, with less than 50% error, but that the target strengths obtained for the models were considerably lower than those obtained for the fish. Using rubber and plastic cylinders to model the backbone and copper cylinders to model the swim bladder, Haslett has examined variations in the target strength of these models as frequency, size, and aspect are varied. A brief summary of Haslett's work for side aspect is shown in Figure 3. Along with his data for the acoustic cross-sections of sticklebacks and guppies, approximations to the acoustic cross-sections of the swim bladder, body, and backbone are given. The various curves for each component were determined by Haslett (1965) using his reflection coefficients and the results of his modeling experiments and depend

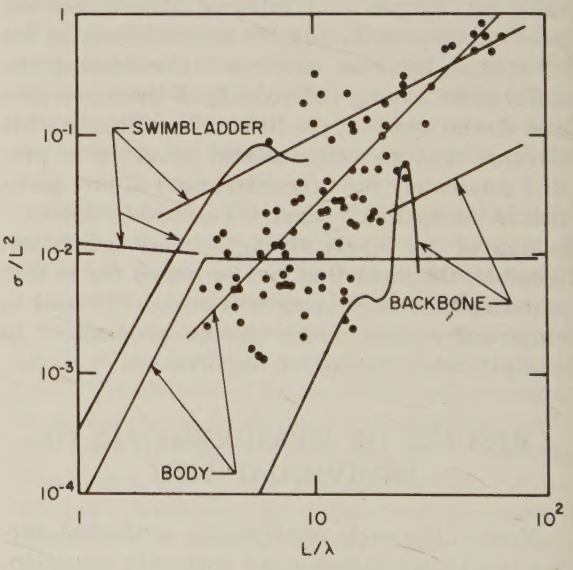

FIGURE 3.—Side-aspect acoustic cross-sections determined by Haslett.

on how the component is approximated and on the limits of that approximation. Hence the curves are a function of whether the swim bladder is approximated by a spherical bubble or a rigid cylinder; what the limits of the geometric and Rayleigh scattering regions are for the body and the backbone; and whether the body is approximated by an ellipsoid or a plane in the geometric region. These curves indicate that the swim bladder predominates over most of the given L/λ range, but that the body and backbone become significant at the higher L/λ's. It is apparent that Haslett's measurements of the acoustic cross-sections of sticklebacks and guppies vary widely and do not follow any of his curves. This variability is not fully explained by any of his experiments on fish or models. Obviously, the nature of the echo-formation process is quite complex if Haslett cannot explain this variability after such comprehensive work.

In attempting to quantify fish resources the objects of interest are usually fish schools rather than individual fish. When the target strength of a school is measured, the question to be answered is "What is the average size and number of fish required to produce this target strength?" The answer will depend on the average target strength of the fish in the school, and any variations among the individuals will be of minor importance. If a forward-looking sonar is used for quantification, the minimum size and number of fish required to produce a given target strength will occur at the aspect for which the target strength of an individual fish is a maximum. This aspect will be near the side aspect of the fish. Thus, average values for the maximum side-aspect target strength of an individual fish are important for quantification of fish schools with a forward-looking sonar. If a downward-looking sonar, or echo sounder, is used for quantification, average values for the dorsal-aspect target strength of an individual fish are important.

For these reasons the author has made maximum side-aspect (Love, 1969) and dorsal-aspect (Love, 1971) target strength measurements as a function of fish size, species, and frequency. The measurements were made in the laboratory, and hollow rubber spheres were used as reference targets for calibration. It was found that the magnitude of the variation in target strength for one species was of the same order as it was for all species. Therefore the data for all species were combined with all other available pertinent data and a regression line was calculated for each aspect using the method of least squares.

Figure 4 shows all the dorsal aspect data. The data were obtained using fish from 16 families in 8 different orders: Clupeiformes, Cypriniformes, Gasterosteiformes, Cyprinodontiformes, Mugiliformes, Gadiformes, Beryciformes, and Perciformes. The fish ranged in length from about 1 cm to 1 m. Some had swim bladders while others did not. Insonifying frequencies ranged from 8 kHz to 1480 kHz. Note that the parameters used here are σ/λ^2 and L/λ, which differ slightly from those used by Haslett. The equation for the regression line calculated from these data is

$$\sigma/\lambda^2 = 0.041\ (L/\lambda)^{1.94}, \qquad (9)$$

and the dorsal-aspect target strength is

$$T_D = 19.4 \log L + 0.6 \log \lambda - 24.9 \qquad (10)$$

Equation (10) is for T_D at 1 m and L and λ in meters and is valid in the range $0.7 \leqslant L/\lambda \leqslant 90$.

Figure 5 shows all the maximum side-aspect data. The data were obtained using fish from 13 families in 7 different orders: Cypriniformes, Gasterosteiformes, Cyprinodontiformes, Gadiformes, Beryciformes, Perciformes, and Pleuronectiformes. Fish size and acoustic frequency ranges were approximately the same as those for dorsal aspect. The equation for the regression line calculated from these data is

$$\sigma/\lambda^2 = 0.064\ (L/\lambda)^{2.28}, \qquad (11)$$

and the maximum side-aspect target strength is

$$T_S = 22.8 \log L - 2.8 \log \lambda - 22.9 \qquad (12)$$

Equation (12) is valid in the range $1 \leqslant L/\lambda \leqslant 130$, and again T_S is at 1 m and L and λ are in meters.

Figure 6 is a nomogram solving equations (10) and (12), given the acoustic frequency, f, in kHz, and the fish length, L, in cm.

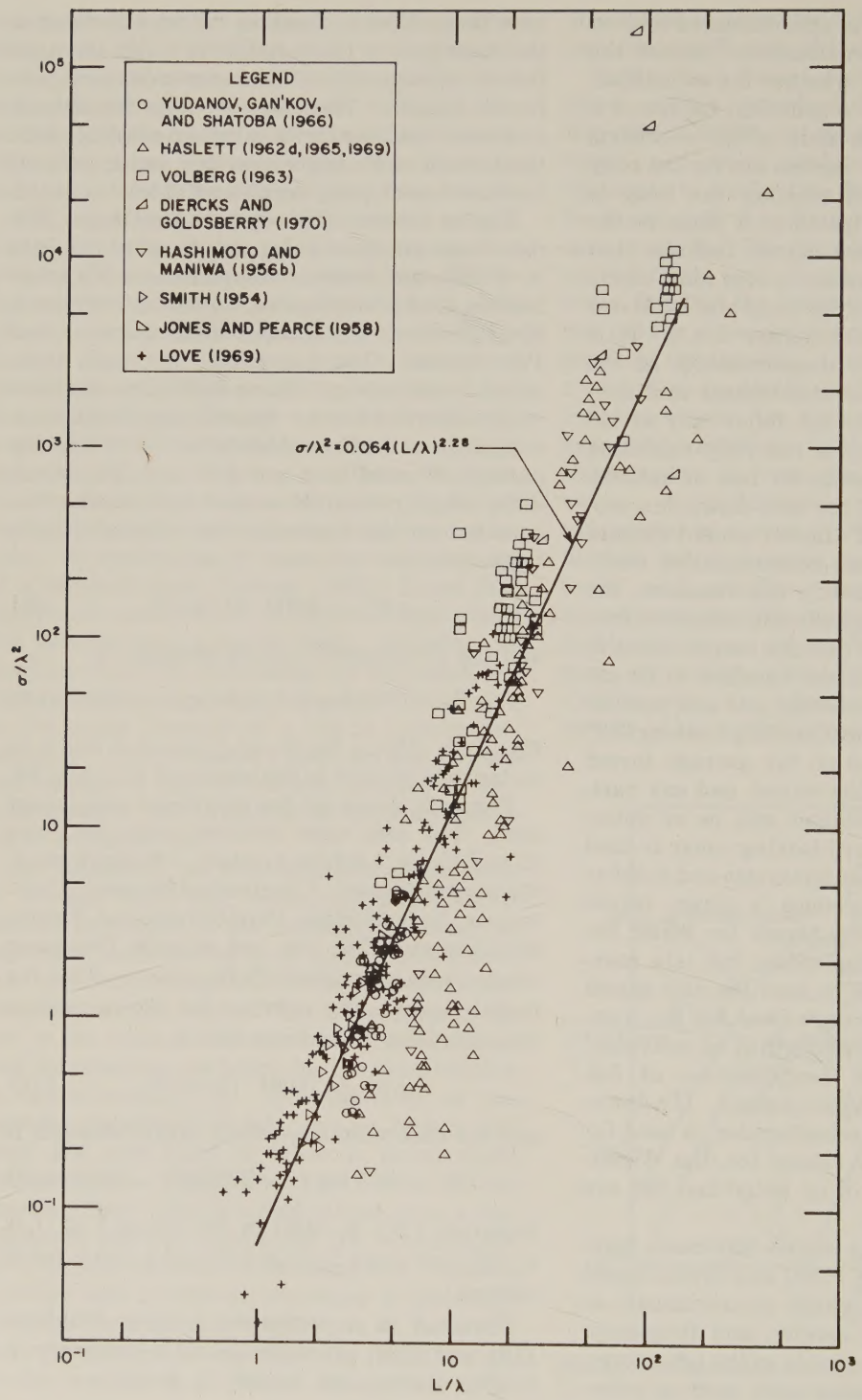

FIGURE 4.—Dorsal-aspect acoustic cross-section of an individual fish.

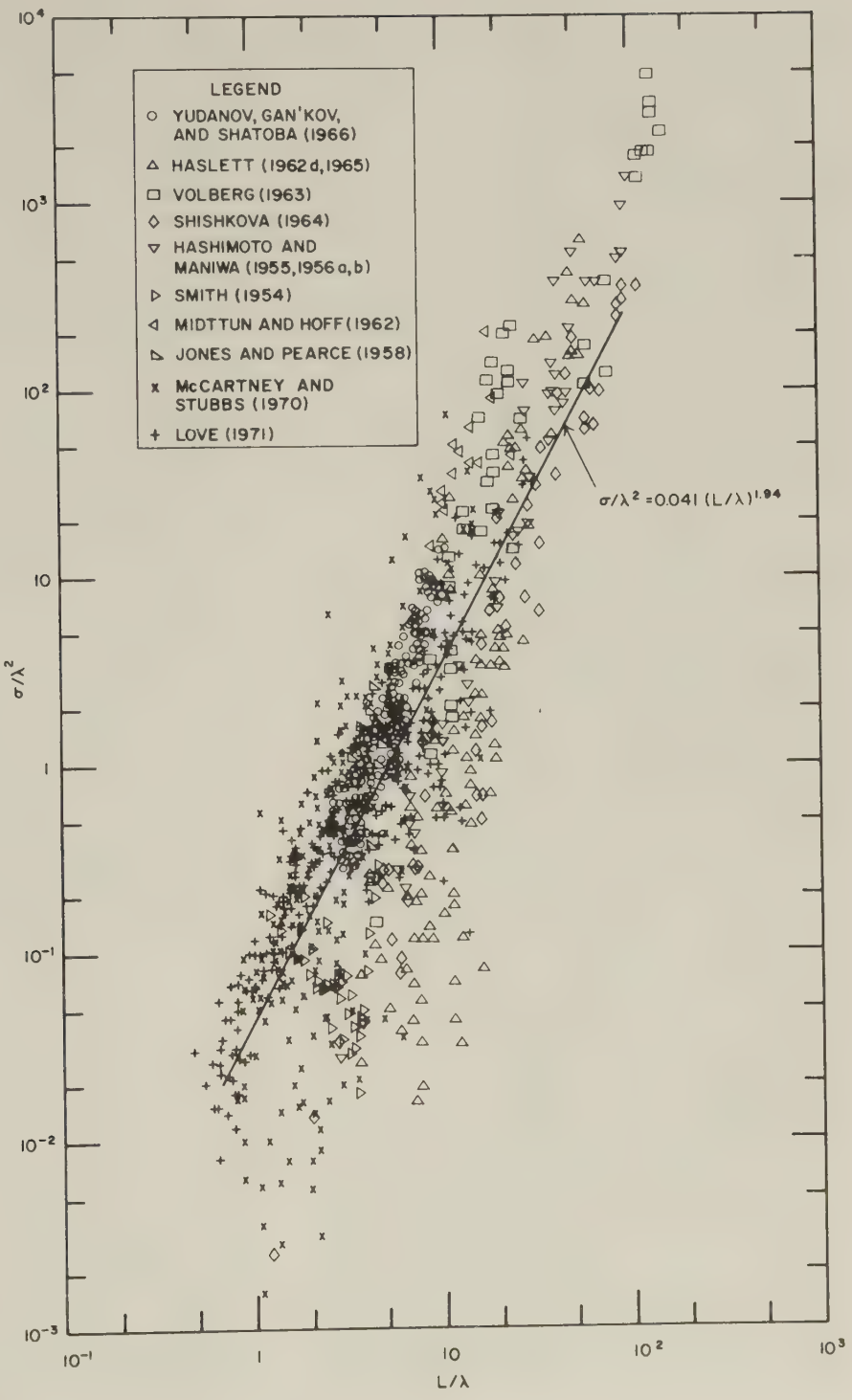

FIGURE 5.—Maximum side-aspect acoustic cross-section of an individual fish.

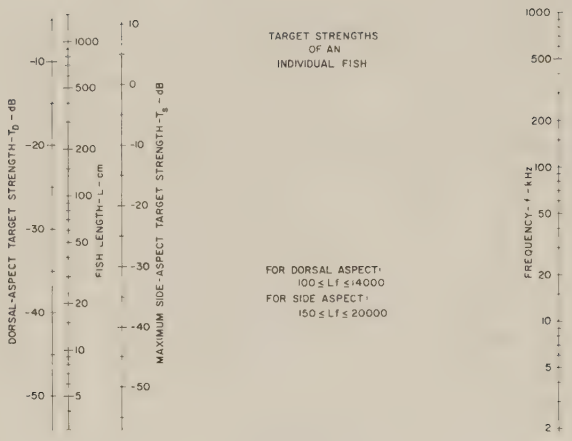

FIGURE 6.—Nomogram for calculating the dorsal-aspect and maximum side-aspect target strengths of an individual fish.

QUANTIFICATION AND IDENTIFICATION OF SCHOOLS

Since estimates for the maximum side-aspect and dorsal-aspect target strengths of individual fish are available, the determination of the target strengths of fish schools at these aspects will depend on the determination of the effects of the number of fish in the school and their distribution. If the fish are widely spaced, or in a plane perpendicular to the sonar beam, so that there is no acoustic interaction among the individuals, the target strength of the school is equal to the average target strength of an individual plus 10 times the logarithm of the number of fish. The probability of finding a school that meets these qualifications is quite small and therefore the effects of interactions among the fish must be taken into account.

Little experimental work on the acoustic interactions of fish in a school has been done, although some measurements of the target strengths of groups of fish have been made, usually with little concern for the distribution of the individuals (e.g., Thorpe and Ogata, 1967; Shishkova, 1960). Some theoretical work on distributions of scatterers has been done, the scatterers usually being point scatterers or small bubbles (e.g., Foldy, 1945; Weston, 1966). Weston (1967) has applied the results for bubbles to fish schools and has estimated reflection coefficients for regions well-below and well-above resonance. Since there is no interference region for a bubble, he does not concern himself with interference effects, and his results are of limited value in the interference region. Boyles (1969) has discussed the mathematical theory of multiple scattering from fish schools, but to obtain results in the interference region the complete spatial scattering and absorption pattern of an individual fish must be known.

The identification of a school of fish utilizing target strength information is obviously much more difficult than its quantification, and since it is not yet possible to quantify fish schools with this information, it is surely not yet possible to identify them.

Figure 3, which summarized Haslett's work, seems to indicate that no reasonable pattern of target strength vs. frequency can be found for any species due to the rapid fluctuations of target strength. Haslett's measurements were made at three widely spaced frequencies. Measurements made by the author at a larger number of more closely spaced frequencies indicate that for individual fish these fluctuations are not so rapid and that possibly individual fish may be identified through the use of target strength vs. frequency (σ/L^2 vs. L/λ) curves. Dorsal aspect target strength measurements made on six bay anchovies, *Anchoa mitchilli*, one Atlantic menhaden, *Brevoortia tyrannus*, five goldfish, *Carassius auratus*, and six Atlantic silversides, *Menidia menidia*, revealed that all of these fish had similar σ/L^2 vs. L/λ curves (Love, 1971). The most notable feature of these curves is a deep minimum in the neighborhood of $L/\lambda = 10$. This minimum is easily seen in the average curves for each species shown in Figure 7. Similar measurements on three mummichogs, *Fundulus heteroclitus*, five striped killifish, *Fundulus majalis*, six black crappies, *Pomoxis nigromaculatus*, and four spotted seatrout, *Cynscion nebulosus*, revealed that the σ/L^2 vs. L/λ curve for any individual of these species bears no easily discernible relation to that of most, or all, of the other individuals of that species, or to the average curve for that species.

The anchovies, goldfish, and menhaden are

malacopterygians, the more primitive teleosts; the crappies and seatrout are acanthopterygians, the more advanced teleosts; and the mummichogs, killifish, and silversides belong to intermediate orders which have characteristics of both groups (Berg, 1947; Bertin and Arambourg, 1958). In general, the malacopterygians have physostomous swim bladders, osseous bone tissue, intermuscular bones, comparatively many vertebrae, fins without spines, and cycloid scales. In general, the acanthopterygians have physoclistous swim bladders, osteoid bone tissue, no intermuscular bones, comparatively few vertebrae, fins with spines, and ctenoid scales. Considering that the swim bladder, bones, and possibly scales of a fish contribute to its acoustic cross-section, it is obvious that the malacopterygians and the acanthopterygians have significant structural differences in components which have been shown to be acoustically important. Why the malacopterygians and one intermediate species display the characteristic minimum in σ/L^2 near $L/\lambda = 10$, or why the acanthopterygians and the other two intermediate species have no distinctive σ/L^2 vs. L/λ curve cannot be answered, given the present limited knowledge of echo-formation by fish.

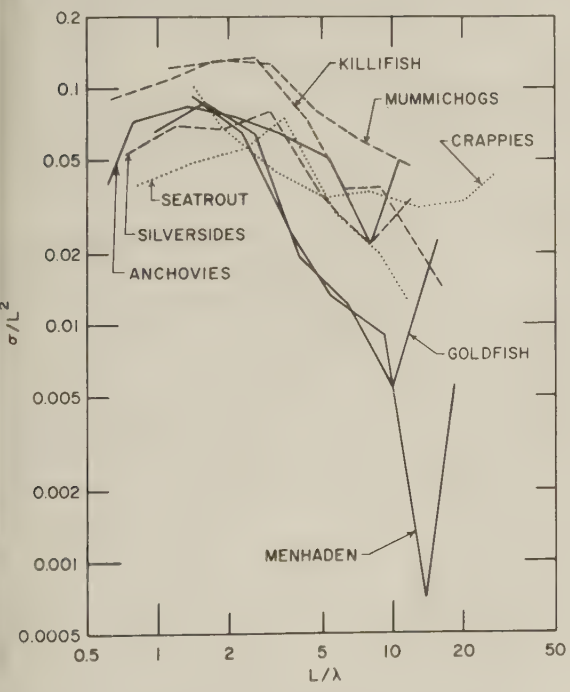

FIGURE 7.—Average measured dorsal-aspect acoustic cross-sections for different species of fish. (From Love, 1971.)

Although these differences cannot be presently explained it seems probable that if there were a geographic area in which two species with about the same size and habits predominated, and if one species were a Clupeiform and the other a Perciform, a ship with a wide-band sonar could differentiate between individuals of each species by examining their target strength vs. frequency curves. This hypothetical example indicates how very limited the present capability to identify fish by determining target strength is. Hopefully, more measurements at many frequencies, with dissection and removal of various components of the fish, and more sophisticated modeling techniques will explain the features of the target strength vs. frequency curves for individuals of a few species. This could then lead to the prediction of curves for other species, which in turn could greatly increase the ability to differentiate between individuals of different species. This information could then be applied to the differentiation of schools of different species, although it is to be expected that the manner of distribution of the fish in the school will cause significant differences between the target strength vs. frequency curve obtained for the school and the average curve for the individuals in the school.

SUMMARY

Some of the more important results of measurements of fish target strength to date are: (1) it has been determined that practically every case of interest to the fishing industry is in the region of interference effects, (2) the major contributors to the target strength of a fish in this region have been determined and their acoustic impedances measured, (3) the variations of target strength with aspect for an individual fish have been examined, (4) estimates of the dorsal-aspect and maximum side-aspect target strength of an individual fish have been made, (5) there

are indications that the identification of individual fish based on target strength vs. frequency curves is possible for limited cases.

The two goals of fish target strength measurements, namely quantification and identification of fish schools, have not yet been attained. The quantification of fish schools and the identification of many individual fish should be hopefully accomplished in the next few years. The identification of schools will require the information on quantification of schools and identification of individuals, and therefore will probably not be accomplished for some time.

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DISTRIBUTION AND BIOLOGY OF MYSIDS (CRUSTACEA, MYSIDACEA) FROM THE ATLANTIC COAST OF THE UNITED STATES IN THE NMFS WOODS HOLE COLLECTION

ROLAND L. WIGLEY AND BRUCE R. BURNS[1]

ABSTRACT

Nineteen species of marine mysids, representing 16 genera, have been assembled at the NMFS Biological Laboratory, Woods Hole, Mass. These specimens were collected between 1953 and 1969 from the continental shelf and slope off the east coast of the United States between Canada and southern Florida. The species represented are: *Eucopia grimaldii, Boreomysis tridens, Bowmaniella portoricensis, Anchialina typica, Erythrops erythrophthalma, Meterythrops robusta, Hypererythrops caribbaea, Pseudomma affine, Pseudomma* sp., *Amblyops abbreviata, Bathymysis renoculata, Mysidopsis bigelowi, M. furca, Promysis atlantica, Mysis mixta, M. stenolepis, Praunus flexuosus, Neomysis americana,* and *Heteromysis formosa.*

Geographic and bathymetric distributions, relations with bottom sediments, and other ecological information are given for all species. Biological data such as spawning season, clutch size, body length at maturity, and similar information are reported for 11 species. More detailed accounts of the life history and ecology of *Erythrops erythrophthalma, Mysidopsis bigelowi,* and *Neomysis americana* are made possible by the large numbers of specimens of these species.

This report is based on the collection of mysids assembled by the Food Habits Project and the Benthic Invertebrates Project at the National Marine Fisheries Service (NMFS), Biological Laboratory—formerly known as the Bureau of Commercial Fisheries (BCF)—Biological Laboratory, Woods Hole, Mass. Mysids were not specifically sought in assembling this collection; they were acquired from biological samples collected for ecological studies pertaining to various kinds of demersal fishes and assemblages of benthic invertebrates. Estuarine and inshore species are few because nearly all sampling was conducted in offshore areas.

The known mysidacean fauna off the eastern coast of the United States is not extensive. Tattersall (1951) made a thorough review of the literature and the mysid specimens in the U.S. National Museum. He reported only 11 shallowwater (less than 200 m) species occurring in the area between Maine and Florida. This includes estuarine and shore forms as well as middle and outer continental shelf species. Although a few additional species have been found in this area since the time of Tattersall's study (Klawe, 1955; Bowman, 1957, 1964; Wigley, 1963; Băcescu, 1968; Haefner, 1968; and others) and undoubtedly some species remain undetected, it is reasonable to conclude that only a modest number of different kinds of mysids occur in this region.

A substantial portion of the species in the NMFS samples from the western Atlantic also occur in European waters. They are: *Eucopia grimaldii, Boreomysis tridens, Erythrops erythrophthalma, Meterythrops robusta, Pseudomma affine, Amblyops abbreviata, Mysis mixta, Praunus flexuosus,* and *Heteromysis formosa.* Those species that do not have an amphi-Atlantic distribution are largely indigenous to the western North Atlantic, namely: *Bowmaniella portoricensis, Hypererythrops caribbaea, Pseudomma* sp., *Bathymysis renoculata, Mysidopsis bigelowi, M. furca, Mysis stenolepis,* and *Neomysis*

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americana. These indigenous species are all inhabitants of warm-temperate to tropical areas; none are subarctic or boreal. Presumably members of this group have been unable to bridge the ocean because of unfavorable water temperatures across the northern rim of the Atlantic Ocean where water depths are favorable. *Amblyops abbreviata* and *Meterythrops robusta*, in addition to having an amphi-Atlantic distribution, are also widely distributed in the North Pacific Ocean. Only *Anchialina typica*, which occurs in the Atlantic and Pacific Oceans, and *Promysis atlantica*, which occurs in the North and South Atlantic Oceans, do not fall into the two main categories above.

The European species *Praunus flexuosus*, now well established in the coastal waters of New England, may have been introduced rather recently by the activities of man (discussion on pages 735 and 736).

The information presented herein supplements our scanty knowledge of the biology of individual species and also provides a general review of the kinds of mysids in the western Atlantic, their distribution, relative abundance, and relations with some environmental characteristics.

MATERIALS AND METHODS

Three million specimens representing 19 species and 16 genera were collected during 1953-69 from the continental shelf and slope off the eastern coast of the United States between Canada and southern Florida.

Two-thirds of the samples were collected from the offshore New England region, between Nova Scotia, Canada, and Long Island, N.Y. (Figure 1). About 2,000 samples were analyzed from this region. Sparse sampling (1,000 samples) was conducted between New York and Key West, Fla. Most of the collections were taken by six oceanographic research vessels: *Albatross III*, *Albatross IV*, *Blueback*, and *Delaware*, all operated by the National Marine Fisheries Service; and *Asterias* and *Gosnold*, operated by the Woods Hole Oceanographic Institution, Woods Hole, Mass. Collection data and biological information for each sample of mysids in the NMFS collection are given in Burns and Wigley.[2] The collection data include: latitude and longitude, water depth, date, sampling gear, vessel name, cruise and station number. The biological information consists of the number of specimens, summary of body length by species, sex, and stage of maturity.

The 12 kinds of sampling instruments used in collecting mysids were: bottom skimmer, Campbell grab, dip net, 30-cm ring net, 1-m ring net, plankton net, naturalists dredge, otter trawl, sled-mounted ring net, Smith-McIntyre grab, shrimp trawl, and Van Veen grab. A few specimens were obtained from fish stomachs. The kinds of gear most successful in catching mysids were ring nets, grab samplers, the bottom skimmer (a combination dredge and plankton net), and dredges with fine-mesh nets. Only occasional specimens were obtained with bottom trawls and dredges with coarse mesh nets.

Mysids were preserved in Formalin at sea and transferred to ethyl alcohol at the time the samples were sorted in the laboratory ashore.

In classifying larvae according to their stage of development, we have followed Nair (1939).

A total of 5,566 specimens were examined under low-power magnification with a binocular microscope to determine sex and stage of maturity and to measure size. Body length was measured from the anterior margin of the carapace to the posterior end of the telson, using an ocular micrometer in the microscope.

SYSTEMATIC ARRANGEMENT

For the systematic arrangement and terminology we have followed Tattersall and Tattersall (1951). The list of species in their respective groupings are as follows:

[2] Burns, Bruce R., and Roland L. Wigley. 1970. Collection and biological data pertaining to mysids in the collection at the BCF Biological Laboratory, Woods Hole. Lab. Ref. No. 70-2, 36 p. Bur. Commer. Fish. Biol. Lab., Woods Hole, Mass. (Unpublished manuscript.)

FIGURE 1.—Chart of the Atlantic Continental Shelf and adjacent area showing the location of sampling stations. A. Samples collected with dredges and similar types of collection instruments. B. Samples collected by means of grab samplers.

Order MYSIDACEA

Suborder LOPHOGASTRIDA

Family EUCOPIIDAE

Eucopia grimaldii Nouvel, 1942

Suborder MYSIDA

Family MYSIDAE

Subfamily BOREOMYSINAE

Boreomysis tridens G. O. Sars, 1870

Subfamily GASTROSACCINAE

Bowmaniella portoricensis Băcescu, 1968

Anchialina typica (Krøyer, 1861)

Subfamily MYSINAE

Tribe ERYTHROPINI

Erythrops erythrophthalma (Goës, 1864)

Meterythrops robusta S. I. Smith, 1879

Hypererythrops caribbaea Tattersall, 1937

Pseudomma affine G. O. Sars, 1870

Pseudomma sp.

Amblyops abbreviata (M. Sars, 1869)

Tribe LEPTOMYSINI

Bathymysis renoculata Tattersall, 1951

Mysidopsis bigelowi Tattersall, 1926

Mysidopsis furca Bowman, 1957

Promysis atlantica Tattersall, 1923

Tribe MYSINI

Mysis mixta Lilljeborg, 1852

Mysis stenolepis S. I. Smith, 1873

Praunus flexuosus (O. F. Müller, 1776)

Neomysis americana (S. I. Smith, 1873)

Tribe HETEROMYSINI

Heteromysis formosa S. I. Smith, 1873

SPECIES ACCOUNTS

Order MYSIDACEA

Suborder LOPHOGASTRIDA

Family EUCOPIIDAE

Eucopia grimaldii Nouvel, 1942

This mysid is a moderately large bathypelagic species that occurs most commonly at depths of about 2,000 m and has not been found at less than 300 m. Its geographic distribution is cosmopolitan, it having been reported from the North and South Atlantic, Pacific, and Indian Oceans. The majority of records are from temperate and tropical waters, but it has been recorded from as far north as Iceland and southern Greenland and as far south as South Africa and New Zealand (Fage, 1942; Tattersall, 1951).

There is only one specimen of *E. grimaldii* in our collection (Burns and Wigley, Table 2), taken at a deepwater station (700 m) along the continental slope off southern New England (Figure 2). This specimen was caught in a 12.2-m shrimp trawl equipped with a coarse-mesh (6.5 cm extension measure) net. Although the net was fished on bottom, it cannot be determined at what depth the specimen occurred. The low fishing efficiency of this trawl during setting and retrieval, however, lends support to the belief that it was caught on or near the ocean bottom.

This is only the second record of this species from off the eastern coast of the United States, even though it is moderately common in other areas and widely distributed throughout the world. Its occurrence in deep water over bottom sediments composed of silts and clays is typical for this species.

Suborder MYSIDA

Family MYSIDAE

Subfamily BOREOMYSINAE

Boreomysis tridens G. O. Sars, 1870

This is a moderately large species that is known to occur only in the North Atlantic Ocean. It is distributed along the eastern Atlantic Continental Slope from the Bay of Biscay

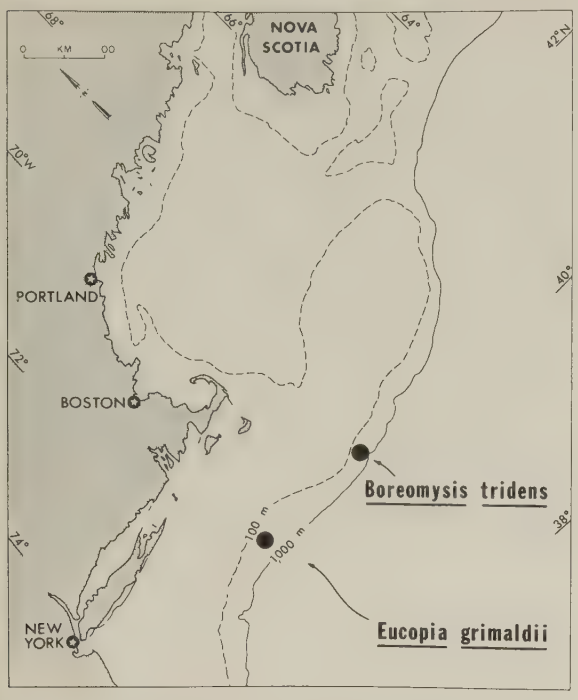

FIGURE 2.—Geographic distribution of *Eucopia grimaldii* and *Boreomysis tridens* based on specimens in the collection at the NMFS Biological Laboratory, Woods Hole.

north to Norway, across to the Faroe Islands, south and west of Iceland and Greenland, southward along the continental slope of North America (Tattersall and Tattersall, 1951). Tattersall (1951) lists over 20 records from off the northeast coast of the United States, ranging as far south as Delaware (lat 38°27′ N).

This species was reported by Verrill (1885) as being common on the continental slope in the western Atlantic. The collections of this mysid reported by Tattersall (1951), all made by the research vessels *Albatross, Fish Hawk,* and *Challenger,* reflect its deepwater habitat.

Our collection contains one sample of this species consisting of three specimens (Burns and Wigley, Table 3). They were taken on the west side of Hydrographer Canyon, located about 130 km southeast of Nantucket, Mass. (Figure 2). The depth of water at this location is 402 m. Its occurrence at this depth and on bottom sediments of silty sand are characteristic for this species. Two specimens 15.0 and 16.5 mm in length are immature; a 26-mm specimen is an adult male.

Subfamily GASTROSACCINAE

Bowmaniella portoricensis Băcescu, 1968

B. portoricensis is morphologically very similar to *B. johnsoni* (Tattersall). A close examination of pleopod 3 in male specimens and of the uropod and the posterior part of the carapace in all specimens was required for reliable differentiation of these two species. *B. portoricensis* is a subtropical species that has been reported by Băcescu (1968) off the southeastern coast of the United States between Beaufort, N.C., and northern Florida. Although this species was known in only a few locations at the time of Băcescu's report, it is undoubtedly more common than these few published records suggest, as indicated by the relatively large number of samples in the NMFS collection. Its rather small size (up to 11-mm body length) and its occurrence in areas that have not yet been thoroughly studied presumably have contributed to the paucity of collections.

The NMFS collection contains 100 specimens of *B. portoricensis* from 46 samples, all of which are from off the southeastern coast of the United States (Figure 3; Burns and Wigley, Table 4). The northernmost samples were taken approximately 90 km north of Cape Hatteras, N.C., at lat 36° N. The southern limit of our samples is 15 km south of Ft. Pierce, Fla., at lat 27°20′ N. All of these samples were collected within 125 km of the shoreline. Water depths at which they occurred range from 9 to 56 m, and most of them were taken at depths between 15 and 39 m.

Body lengths average 6.9 mm; the range in length is 3.1 to 10.0 mm.

This species is chiefly an inhabitant of sandy sediments. Sand was present at all stations. Shell was a major component at 7% of the stations and a minor component at 26% of the stations where *B. portoricensis* occurred.

Seven females, 7.9 to 10 mm in length, from the May and June samples were carrying larvae in the brood pouch. The number of larvae per clutch ranges from 1 (obviously an incomplete brood) to 30. Only the relatively advanced

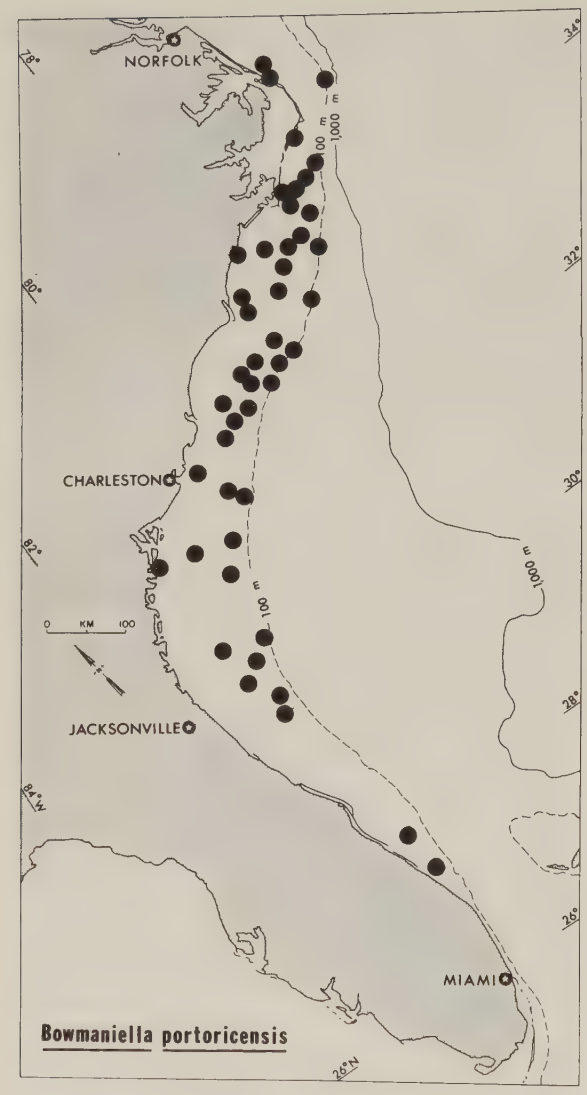

FIGURE 3.—Geographic distribution of *Bowmaniella portoricensis* based on specimens in the collection at the NMFS Biological Laboratory, Woods Hole.

larval stages—V, VI, and VII, with lengths from 1.0 to 1.2 mm—are represented. The presence of larvigerous females as well as immature specimens in May and June samples reveals that *B. portoricensis* spawns not only in early summer, but in the springtime as well.

The NMFS collection contains 31 males and 47 females, a ratio of 0.7 male to 1 female.

Anchialina typica (Krøyer, 1861)

This moderately small, stout mysid is widely distributed in both the Atlantic and Pacific Oceans. It has been reported from the Pacific near the central (Hawaii and Gilbert Islands) and southwestern (China Sea to Great Barrier Reef) regions. According to Tattersall (1951) it is abundant in the region of the Philippine Islands and the East Indies. Though it has been reported in the North Atlantic from south of Newfoundland (Nouvel, 1943), records from the vicinity of the Bahama Islands and Cuba are the most common. Many occurrence records in the literature are based on specimens collected in surface waters.

The NMFS collection contains three specimens from three different stations (Figure 4;

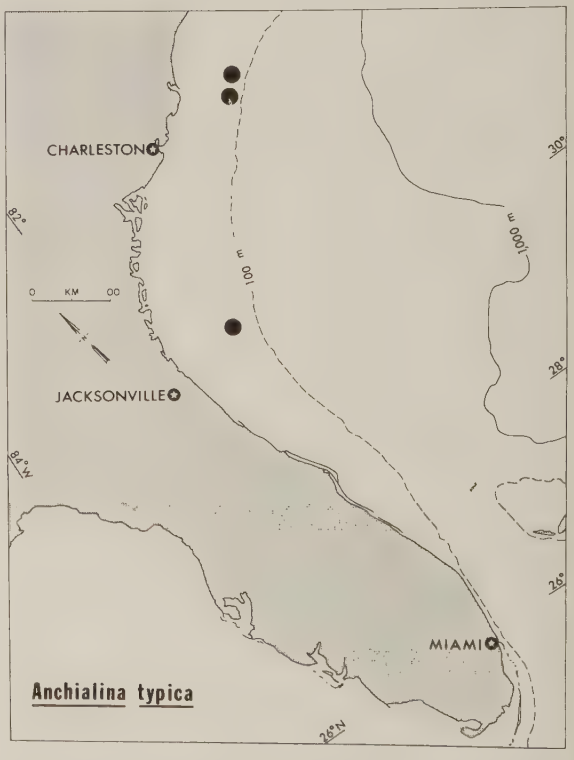

FIGURE 4.—Geographic distribution of *Anchialina typica* based on specimens in the collection at the NMFS Biological Laboratory, Woods Hole.

Burns and Wigley, Table 5). The southernmost sample is from off northern Florida. The other two samples were taken 60 to 70 km east of Georgetown, S.C. All specimens are males 4.5 to 5.0 mm long. They were all collected with the Campbell grab in rather shallow water, between 32 and 38 m. Bottom sediments at these stations are composed of fine and medium sand. These are the first records of this genus and this species from the shallow shelf region off the eastern coast of the United States.

A closely related species, *A. agilis,* is an active swimmer that migrates to surface waters at night and descends to deep water before daybreak (Russell, 1925). Based on NMFS records of *A. typica* reported herein, and on Tattersall's (1951) records, it appears likely that *A. typica* in the shallow and moderately shallow regions of the continental shelf may also dwell on bottom during the day and rise to surface or near surface waters at night.

Subfamily MYSINAE

Tribe ERYTHROPINI

Erythrops erythrophthalma (Göes, 1864)

Geographic Distribution

This colorful mysid species has a widespread distribution on the continental shelf and upper portion of the continental slope in Arctic seas and the North Atlantic Ocean. In eastern Atlantic waters it extends from the Arctic southward to the British Isles. In the western Atlantic it has been reported from off Greenland, eastern Canada, and off the northeastern United States as far south as Delaware (Gardiner, 1934; Bigelow and Sears, 1939; Tattersall, 1951; Tattersall and Tattersall, 1951).

The NMFS collection contains 187 samples totaling 4,573 specimens of this species (Figure 5; Burns and Wigley, Table 6). These samples were collected on the continental shelf and slope between southeastern Nova Scotia and Long Island, N.Y. By far the largest number of samples is from the southern part of Georges Bank. A moderate number of samples were taken in the offshore southern New England area south

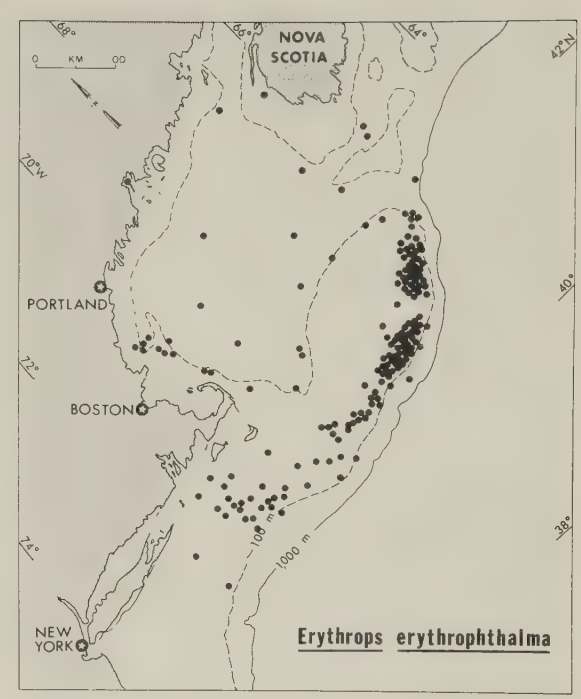

FIGURE 5.—Geographic distribution of *Erythrops erythrophthalma* based on specimens in the collection at the NMFS Biological Laboratory, Woods Hole.

of Rhode Island and eastern Massachusetts. The common occurrence of this species on Georges Bank was somewhat unexpected in view of the fact that Whiteley (1948) found it to be a minor component in plankton samples collected there in 1939-41.

Bathymetric Distribution

This is an offshore species that occurs chiefly in mid- to outer-shelf depths. The shallowest record in published accounts that we have seen is 12 m, reported by Procter (1933) for specimens collected on the coast of Maine. Deepest record previously reported is 275 m, from the Gulf of St. Lawrence (Tattersall, 1957). Depth range for samples in the NMFS collection is 18 to 421 m (Table 1).

A large proportion (78% of the samples and 90% of the specimens) were taken at midshelf depths, 60 to 100 m. The sample from unusually

TABLE 1.—Bathymetric distribution of *Erythrops erythrophthalma*, based on the NMFS collection.

Water depth	Samples	Specimens
m	*Number*	*Number*
0- 19	1	1
20- 39	1	2
40- 59	13	277
60- 79	73	1,676
80- 99	72	2,422
100-119	12	133
120-139	4	6
140-159	4	33
160-179	3	17
180-199	1	1
200-219	1	2
220-239	1	1
420-439	1	2
Total	187	4,573

deep water was collected at the head of Lydonia Canyon, along the southwestern edge of Georges Bank. This sample consisted of two specimens, one adult female and an immature, collected in a stramin-mesh ring net towed 1 to 2 m above the sea bottom.

Spawning

Seven ovigerous specimens are present only in the August samples, and 11 larvigerous specimens are present in August and September samples. This is an unusually small number of specimens (about 1%) in spawning condition compared with the total number of adult females. Furthermore, the spawning females are not especially large. Their average length is 6.4 mm, range 5.7 to 7.1 mm. Larger specimens taken during the same month and at other seasons are not in spawning condition. The presence of immature specimens of about 4 to 5 mm in length throughout the period from June through December implies an extended spawning season during the warmer part of the year, plus the possibility of spawning during other seasons as well. The absence of well-defined length modes from month to month also supports the hypothesis of a lengthy spawning period.

The number of eggs per clutch ranges from 1 to 6, and the number of larvae from 2 to 15. The lower values appear to represent incomplete broods that resulted from losses incurred during the catching and processing procedures.

In summary, the available evidence from the NMFS material suggests that only a small part of the population spawns at one time and that spawning takes place throughout a large part of the year—possibly from spring through fall or longer.

Sex Ratio

The NMFS collection contains 1,536 males and 1,692 females, a ratio of 0.91 male to 1 female.

Body Size

The eggs are nearly spherical and average 0.4 mm in diameter. Larvae of stage V are 1.2 mm long, and stage VII are 1.4 mm. Immatures range in length from 3.0 to 6.1 mm. Mature specimens have an overall size range from 4.3 to 9.6 mm. Size range during various seasons, separated by sexes, are:

Season	Males	Females
Mar.-Apr.	6.4	6.1
May -June	5.2-7.5	5.8-7.0
July -Aug.	5.1-8.3	5.0-9.0
Sept.-Oct.	4.8-9.6	4.3-8.7
Nov.-Dec.	5.1-8.9	5.0-8.9

A size comparison of mature males with mature females from the same samples discloses that males are 0.3 to 0.4 mm larger than females.

The minimum size of adults is generally larger in the early summer, decreases in late summer and fall, then increases again in early winter. This is due to an earlier maturation of immature individuals during the period when water temperatures are comparatively high. The trend for maximum size of adults is just the opposite. Maximum length is smallest in early summer, increases in the late summer and fall, and (the males only) decreases again in early winter. It is not clear whether this sequence in size differences results solely from faster growth during the warm season, or whether a summer generation has reached the culmination of its life span in September-October.

Length of Life

An analysis of body length measurements did not disclose trends in growth or separate length-frequency modes that indicated year classes. Immature specimens with an average length of roughly 4.5 mm are present in June, August, September, November, and December. The mature groups of both males and females in these same months are mostly between 5 and 7 mm long and do not exhibit the expected increases in size as the seasons progress. Our tentative conclusion is that *E. erythrophthalma* has a short life span, a rapid growth rate, and a lengthy spawning season.

Relation to Bottom Sediments

Members of this genus are considered to dwell on or near the sea bottom, and our catch records substantiate this view. It is uncommon in plankton samples collected in the upper water layers, but is regularly taken in hauls collected near bottom. It occurred most frequently and in greatest abundance on sand sediments (Table 2). Seventy-seven percent of the samples and over 90% of the specimens were taken on, or over, sand sediments. A moderate number of samples (10%) were taken in areas of fine-grained sediments. Furthermore, it should be added that most of the sediments along southern Georges Bank, where the majority of samples were taken, contain modest amounts of silt, generally between 1 and 10%. These quantities are insufficient to be incorporated in the bottom type terminology (Shepard, 1954). Although these are small quantitities, the presence of silt on the sediment surface makes it readily available to the mysids. Furthermore, this species is common on the silty sediments in the region south of Martha's Vineyard, Mass. Thus *E. erythrophthalma* appears to inhabit sediments containing a small to moderate amount of silt, in contrast to *N. americana* and *M. bigelowi*, which are more common in sediments having a very low silt content.

TABLE 2.—Frequency of occurrence of *Erythrops erythrophthalma* in various types of bottom sediments, based on the NMFS collection.

Bottom type	Samples	Specimens
	Number	*Number*
Rock-gravel	6	122
Gravel-sand	6	13
Glacial till	2	12
Sand	144	4,224
Sand-silt	12	50
Silt-clay	17	152
Total	187	4,573

Meterythrops robusta S. I. Smith, 1879

This rather large but uncommon species has a wide distribution in boreal and subarctic waters. In the Atlantic region it has been reported from the Kara Sea, Spitsbergen, Norway, Greenland, Gulf of St. Lawrence, and in the Gulf of Maine as far south as Cape Cod, Mass. In the Pacific it occurs in the area between Alaska and Washington. Moreover, assuming that *M. microphthalma* is a synonym for *M. robusta* (see Banner, 1954), then its distribution also includes the region off the east coasts of Japan and Korea (Tattersall, 1951).

The NMFS collection contains nine specimens from six stations, all from the periphery of the Gulf of Maine (Figure 6; Burns and Wigley, Table 7). Four specimens were collected at one station in the channel north of Browns Bank; three specimens were from three stations north of Great South Channel; and two specimens were taken off eastern Massachusetts.

Bathymetric distribution ranged from 64 to 150 m, and all specimens except one were from depths between 110 and 150 m.

The type of bottom sediments inhabited by this species is distinctive. The bottom sediments contained gravel at five of the six stations where *M. robusta* occurred. Three of the samples were taken on glacial till; one sample was from sandy gravel; one sample was from gravel; and one sample was from silt-clay. All other offshore species of mysids in the NMFS collection are associated with sand or finer grained sediments.

All specimens of *M. robusta* in the NMFS collection were caught in stramin nets or natu-

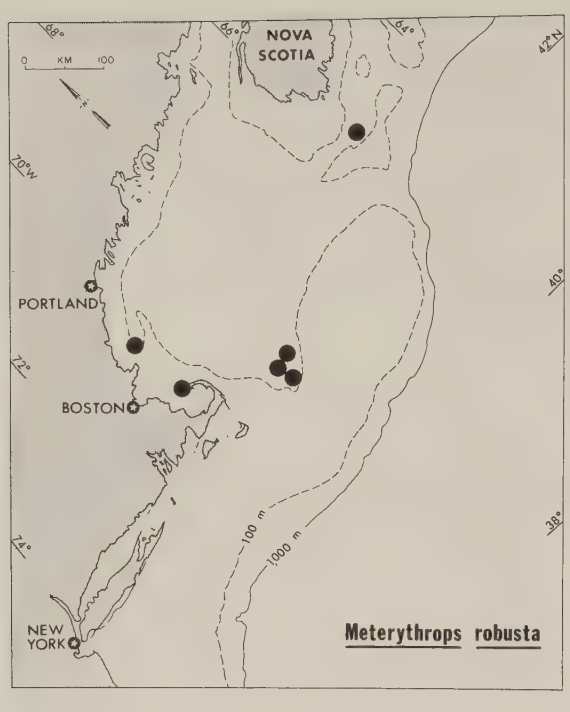

FIGURE 6.—Geographic distribution of *Meterythrops robusta* based on specimens in the collection at the NMFS Biological Laboratory, Woods Hole.

ralists dredges towed along the sea bottom. From this we infer that this species probably inhabits the sea bottom or the water stratum closely adjacent to bottom.

Body length of immature specimens ranged from 6.6 to 7.5 mm, young males 8.5 to 12.0 mm, and young females 8.6 to 9.3 mm. There were no large specimens in the NMFS collection that compare in size with the 28.5-mm adult male reported by Smith (1879) from the Gulf of Maine.

The six adult specimens included four males and two females, a ratio of two males to one female.

No definite information pertaining to spawning is available from the material in our collection. Both females are young and without external eggs. The only evidence on this subject is the presence of immature and young specimens in the August collections, which implies a spring spawning season.

Hypererythrops caribbaea Tattersall, 1937

This species is distributed along the east coast of North America from Maine to the Caribbean Sea. It has been reported from the outer continental shelf and upper slope at depths between 214 to 402 m (Tattersall, 1951). Apparently it is an uncommon species, since it has been reported previously from only seven stations. Body size is moderately small; lengths range from about 8 to 13 mm.

The NMFS collection contains three specimens from three locations (Figure 7; Burns and Wigley, Table 8), between the southern Gulf of Maine and the continental shelf margin south of Rhode Island. This southernmost sample is from a depth of 179 m; the others are from 168 to 179 m. The smallest specimen, 5.5 mm body length, is immature; the other two, 9.5 to 11.0 mm, are adult females. The largest specimen is larvigerous with an incomplete brood

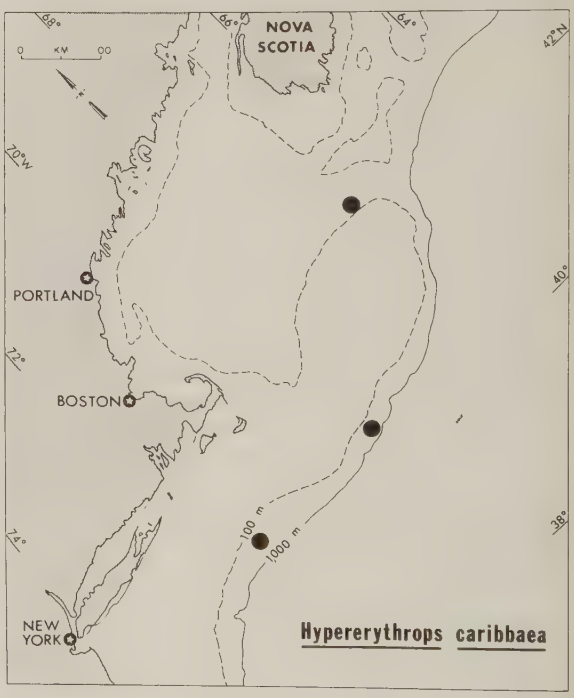

FIGURE 7.—Geographic distribution of *Hypererythrops caribbaea* based on specimens in the collection at the NMFS Biological Laboratory, Woods Hole.

of only two young in the brood pouch. Collection of this specimen in August indicates a summer spawning season for this species. This larvigerous specimen was found in the stomach of a Gulf Stream flounder, *Citharichthys arctifrons* Goode. Since *H. caribbaea* is found in warm-temperate waters, its occurrence in the Gulf of Maine may be restricted to the deeper basin areas where water temperatures are ameliorated by the intrusion of relatively warm, high-salinity slope water.

Pseudomma affine G. O. Sars, 1870

The geographic distribution of this species extends from the Bay of Biscay northward to Norway, westward to Iceland, Greenland, and North America. We found only two records of its occurrence in North American waters. Tattersall (1951) recorded one specimen taken by the research vessel *Fish Hawk* at station 999, located 153 km south of Rhode Island (lat 39°45′ N, long 71°30′ W) at a depth of 487 m. Klawe (1955) reported taking this species 2 km off Campobello Island, New Brunswick, Canada.

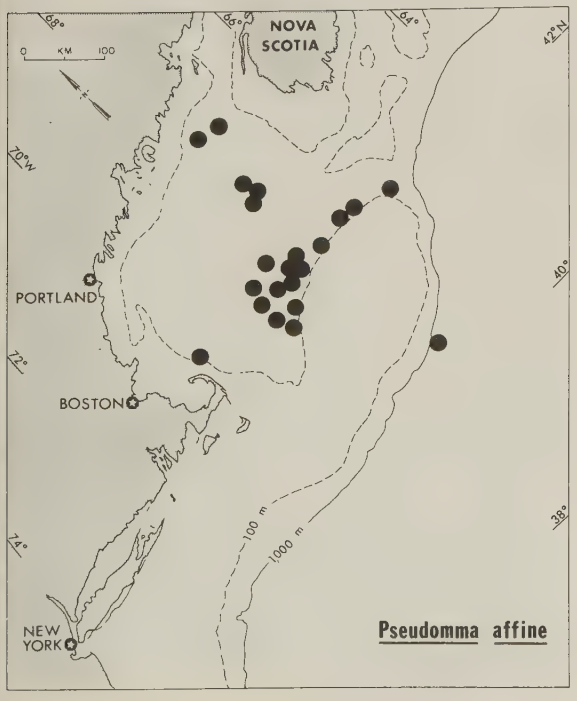

FIGURE 8.—Geographic distribution of *Pseudomma affine* based on specimens in the collection at the NMFS Biological Laboratory, Woods Hole.

Bathymetric range of all records from the North Atlantic Ocean is 80 to 914 m.

Our collection contains 119 specimens from 22 samples (Figure 8; Burns and Wigley, Table 9), all from the Gulf of Maine, except one from just south of Georges Bank. They were collected at moderate water depths: 146 to 329 m. Bottom sediments at these collecting sites contain large proportions of fine particles, chiefly silts, clays, and fine sands. Only two samples were taken in areas having gravel or coarse sand bottom.

Body lengths range from 4.0 to 13.1 mm; the majority are between 8 and 11 mm.

Evidence of an extended spawning season is provided by the presence of ovigerous, larvigerous, and small juvenile specimens in the collection. A 10.9-mm ovigerous specimen was taken in December (*Albatross III*, cruise 70, station 41) with 11 eggs and an average egg diameter of 0.4 mm. One 11.0-mm larvigerous specimen taken in August (*Albatross IV*, cruise 65-11, station 56) contains one larva 1.2 mm long. Additionally, juveniles 5 mm or less in length were taken in August, November, and December. Spawning thus takes place during summer and winter and may also occur in the spring and fall.

Sex ratio of the specimens in the NMFS collection is 2.3 males (68 specimens) to 1 female (29 specimens).

Several morphological features in our specimens differ slightly from published descriptions of this species. In Table 3 are listed the number of spines on the telson and relative length of the antennal scale apex and relative width of the antennal scale. Specimens in our collection have fewer apical spines (nearly always 6) on the telson, and a greater number of spines (9-24, average 17) on the lateral margins of the telson, than specimens from the eastern Atlantic. Also, the antennal scales on Gulf of Maine specimens have a proportionately longer apex (that portion of the scale between the spine cleft and the anterior end) than eastern Atlantic specimens. Spination of the telson and shape of the antennal

TABLE 3.—Number of spines on the telson and the proportional measurements of the antennal scale for individual male and female specimens of *Pseudomma affine* of various sizes.

Body length	Spines on telson		Antennal scale	
	Apex	Lateral[1]	Relative length of apex[2]	Relative width[2]
mm	*Number*	*Number*	%	%
Males				
8.0	6	15	31	29
10.0	6	17	34	25
10.3	6	19	36	27
13.0	8	24	37	29
Females				
4.3	6	9	28	32
7.0	6	13	33	33
7.3	6	--	36	31
10.4	6	21	40	29
10.5	6	19	44	30
12.0	6	18	42	30

[1] Total count of lateral spines from both sides of the telson.
[2] Measurements expressed as percentages of the antennal scale length.

scale change as the specimens increase in size. The number of lateral spines on the telson increases with body length, particularly in males. In both males and females the apex of the antennal scale is proportionately longer in larger specimens.

Sexual dimorphism is rather slight in the characters listed in Table 3. Females have a relatively larger antennal scale apex and a slightly broader antennal scale than males.

The close affinity of *P. affine* with *P. roseum* G. O. Sars necessitated considerable effort to establish the identity of the specimens at hand. In addition to the taxonomic characters mentioned above, specimens in our collection were distinguished from *P. roseum* by: the relatively broad telson and an ocular plate that has a broad, gently rounded anterolateral "corner" with serrations extending along a large portion of the lateral margins. The practice of using morphological characters that change with size or vary according to sex or stage of maturity has led to confusion between these species. Further taxonomic studies of these two species are clearly in order.

Pseudomma sp.

Ten specimens of *Pseudomma* that do not correspond morphologically to any known species are represented from three localities off southern New England. A description of this species and notes on its ecology is being prepared and will be reported elsewhere.

Amblyops abbreviata (M. Sars 1869)

This widely distributed boreal mysid occurs in both the North Atlantic and North Pacific Oceans. In the Pacific it has been found off Japan and off the west coast of North America from Washington to Alaska. In the Atlantic it ranges from the Bay of Biscay north to Scandinavia, west to Greenland and North America. Previous records from the northeastern coast of the United States consist of 38 specimens from 7 offshore stations situated between Cape Cod, Mass., and northern New Jersey. These specimens were collected by the U.S. Fish Commission between 1879 and 1881 at water depths between 238 and 838 m.

Our collection contains 34 specimens from 8 samples taken in the Gulf of Maine, primarily in the southern part of the Gulf (Figure 9; Burns and Wigley, Table 10). Water depths at these localities range from 183 to 329 m. The bottom sediments where these specimens were taken are composed predominantly of silts, clays, and fine sands; one exception is a sandy gravel bottom off the eastern end of Georges Bank where one juvenile specimen was obtained. Body length ranged from 4.7 to 15.0 mm. The size of adults is 10 to 15 mm; the males tend to be slightly larger (average length 12.9 mm) than females (average length 12.3 mm).

Spawning occurs during winter and possibly in other seasons as well. One ovigerous female collected in December (*Albatross III*, cruise 70, station 25) had 29 eggs in the marsupium, each 0.4 mm in diameter. The presence of juvenile specimens 4 to 6 mm in length in August and an 8-mm specimen in December suggests that spawning also takes place in summer and fall.

Sex ratio of the specimens in the NMFS collection is 0.65 male (11 specimens) to 1 female (17 specimens).

FIGURE 9.—Geographic distribution of *Amblyops abbreviata* based on specimens in the collection at the NMFS Biological Laboratory, Woods Hole.

between Hudson Canyon and Hydrographer Canyon—in the same area where they were found to be most common by the *Fish Hawk* and *Albatross* (Figure 10; Burns and Wigley, Table 11). The depth range of their occurrence is 220 to 366 m. Because two samples were collected with the bottom skimmer, it is certain these specimens were present on the sea bottom at the time of capture. Their presence on the bottom during hours of low light level, 1600 to 2200 hr, suggests they may not undertake a diurnal vertical migration. Five specimens are adults, 13.0 to 16.2 mm long, and three specimens are immature, 4.0 to 6.0 mm long. We have no information on spawning other than the presence of 4- to 6-mm specimens in June, from which a spring spawning may be inferred. Bottom sediments at the collecting sites are fine-grained types: sand, silt, and silt-clay.

Tribe LEPTOMYSINI

Bathymysis renoculata Tattersall, 1951

This large-eyed species of *Bathymysis*, which occurs only in the western Atlantic Ocean, has been reported from southern New England to the southern tip of Florida (Tattersall, 1951). The principal area of occurrence is along the outer continental shelf and upper slope between Hudson Canyon and Hydrographer Canyon (southeast of Nantucket, Mass.). The bathymetric range reported for this species is 220 to 483 m. These records are based on collections made by the research vessels *Fish Hawk* and *Albatross* during the latter part of the last century.

The NMFS collection contains eight specimens from three stations off southern New England

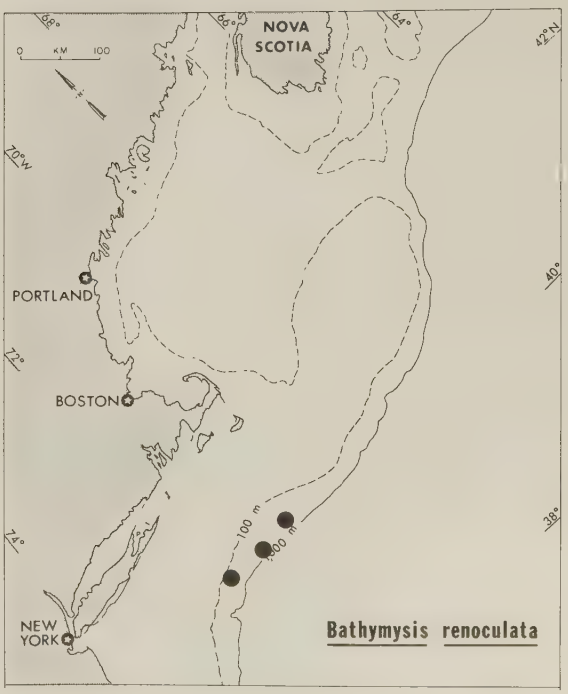

FIGURE 10.—Geographic distribution of *Bathymysis renoculata* based on specimens in the collection at the NMFS Biological Laboratory, Woods Hole.

Mysidopsis bigelowi Tattersall, 1926

Geographic Distribution

M. bigelowi is a small American species that occurs along the Atlantic and Gulf coasts of eastern and southern United States from New England to Louisiana.

The NMFS collection contains 2,031 specimens out of 54 samples (Figure 11; Burns and Wigley, Table 12) collected from northeastern Georges Bank southward along the coast to the vicinity of Jacksonville, Fla. Georges Bank is the principal area represented in the sampling; the results extend the known range of this species a considerable distance to the northeast. Only five samples were from localities south of the Nantucket Shoals region: these were taken off New Jersey, Virginia, North Carolina, and northern Florida.

It is interesting to note this species is not listed as present in the plankton samples collected from Georges Bank between 1939 and 1941 (Whiteley, 1948). Although the absence could have been due to annual fluctuations in abundance in this northern sector of its range, our results show the species was present each year we conducted moderate or heavy sampling: in 1955 through 1958, and in 1964 through 1967. More likely the absence in the 1939-41 samples resulted not from temporary fluctuations but because these earlier collections were primarily from middle and upper water levels, whereas most of the NMFS collections were taken on or near the sea bottom.

Bathymetric Distribution

M. bigelowi is a shallow-shelf species that has been reported from inshore localities such as the inlet to Indian River Bay, Del., and Calcasieu Pass, La., and from offshore waters as deep as

FIGURE 11.—Geographic distribution of *Mysidopsis bigelowi* based on specimens in the collection at the NMFS Biological Laboratory, Woods Hole.

77 m (Tattersall, 1951; Grice and Hart[3]; Hopkins, 1965).

Depth range of the NMFS samples is from 13 to 179 m. By far the largest number of samples (73%), greatest number of specimens (91%), and highest densities occur between 30 and 80 m (Table 4). One collection taken at an unusually deep locality, 179 m, is from the northern edge of Georges Bank. The water circulation in this area and its proximity to shallow waters commonly inhabited by this species may account for its presence at that relatively great depth.

TABLE 4.—Bathymetric distribution of *Mysidopsis bigelowi*, based on the NMFS collection.

Water depth	Samples	Specimens
m	*Number*	*Number*
10- 19	4	28
20- 29	3	10
30- 39	9	557
40- 49	8	493
50- 59	9	640
60- 69	7	73
70- 79	6	85
80- 89	4	22
90- 99	2	116
100-109	1	1
170-179	1	6
Total	54	2,031

Spawning

This species spawns from April to November in the coastal areas of Delaware (Hopkins, 1965). There is no information about spawning habits of the offshore and northern populations, and we did not find a single ovigerous or larvigerous specimen in the NMFS collection. We do, however, have immature specimens represented in samples collected in May, August, September, November, and December. This is indicative of a long spawning season, probably from early summer through fall.

The large size of immatures, 4.0 to 5.0 mm, in May samples is believed to represent the overwintering young. The absence of ovigerous females in the many large samples collected in December is evidence that spawning most likely has terminated by that time of year.

[3] Grice, George D., and Arch D. Hart. 1962. The abundance, seasonal occurrence and distribution of the epizooplankton between New York and Bermuda. Appendix to Ref. 62-4, Woods Hole Oceanogr. Inst. (Unpublished manuscript.)

Sex Ratio

The NMFS collection contains 313 males and 195 females, a ratio of 1.6 males to 1 female.

Body Size

This species is the smallest mysid in the NMFS collection. A summary of body length data by month of capture for males, females, and immatures is given in Table 5. Range in body length among all specimens in the collection is 2.4 to 6.6 mm. The average length of immatures is 3.8 mm, males 4.9 mm, and females 5.1 mm. Members of this species were found to mature at 3.5 mm, smaller than any other species in the NMFS collection.

TABLE 5.—Means and ranges of body length of *Mysidopsis bigelowi* by months and sexes.

Month	Body length					
	Immatures		Males		Females	
	Mean	Range	Mean	Range	Mean	Range
	mm	*mm*	*mm*	*mm*	*mm*	*mm*
May	4.6	4.0-5.0	5.1	4.9-5.7	5.5	5.4-5.7
Aug.	4.0	--	4.9	4.2-6.6	4.5	3.8-5.8
Sept.	3.0	--	4.6	--	5.0	--
Nov.	3.8	2.4-4.1	5.2	4.6-5.7	5.1	4.0-6.3
Dec.	3.5	2.4-4.5	4.8	3.5-5.8	4.5	3.5-5.6

Length of Life

Our samples are inadequate to give an accurate estimate of the length of the life cycle. The few available clues, such as the presumably long spawning season and the large size of the overwintering immatures, are suggestive of a life cycle similar to *Neomysis americana*: a short-lived summer generation and a long-lived winter generation.

Relation to Bottom Sediments

Many specimens in the NMFS collection were taken with bottom samplers (Smith-McIntyre, Van Veen, and Campbell grabs) or gear that

sampled water layers adjacent to the sea bed (sled net). These results suggest *M. bigelowi* lives in or on the bottom sediments during much of its life.

An analysis of the types of bottom sediments at the collecting sites reveals a high incidence of this mysid on various grades of sand (Table 6), usually sand containing little or no silt or clay. They tend to avoid fine-grained sediments as further evidenced by their absence in several hundred samples taken from a 1,000 square km area of predominantly silt and sandy-silt sediments south of Martha's Vineyard, Mass., on research vessel *Delaware* cruise 62-7.

TABLE 6.—Frequency of occurrence of *Mysidopsis bigelowi* in various types of bottom sediments, based on the NMFS collection.

Bottom type	Samples	Specimens
	Number	*Number*
Rock-gravel	4	177
Gravel-sand	1	1
Shell-sand	1	1
Sand	44	1,847
Sand-silt	1	1
Unclassified	3	4
Total	54	2,031

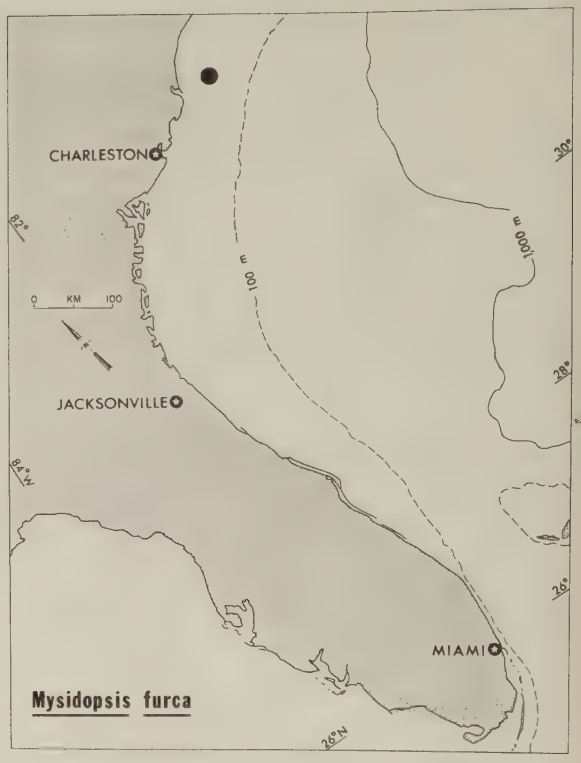

FIGURE 12.—Geographic distribution of *Mysidopsis furca* based on a specimen in the collection at the NMFS Biological Laboratory, Woods Hole.

Relation to Water Temperature

M. bigelowi inhabits water temperatures from about 2° C in the northern part of its range to summer water temperatures of about 30° C in the Florida and Louisiana areas. The annual change in temperature is slightly less than 20° C in the north and slightly more than 20° C in the south.

Mysidopsis furca Bowman, 1957

This species was described by Bowman (1957) from a sample containing 23 specimens collected in 1953 by the research vessel *Theodore N. Gill*. The specimens were obtained at one station (number 57) located 40 km from shore off the northern coast of South Carolina. Depth of water at the collecting site is 22 m. It was later reported by Brattegard (1969) from off southeastern Florida at depths of 1 to 48 m.

The NMFS collection contains one specimen, a female 4.2 mm long, taken with the Campbell grab 50 km east of Georgetown, S.C., (Figure 12; Burns and Wigley, Table 13) about 50 km southwest of the type locality. The specimen was taken at a depth of 22 m on sediment composed of fine sand. This small species has a reported size range of 4.6 to 6.1 mm (Bowman, 1957). Neither the size nor the developmental stage of the NMFS specimen provides any indication of spawning season or size at maturity.

Promysis atlantica Tattersall, 1923

This rare species was described from an immature female specimen collected off Rio de Janeiro, Brazil, in 1910 (Tattersall, 1923). It was not reported again until Clarke (1956) described the male and adult female, and gave new records of occurrence for specimens col-

lected off the coasts of Louisiana, South Carolina, and North Carolina.

The NMFS collection contains three specimens from three stations located off the southeastern coast of the United States (Figure 13; Burns and Wigley, Table 14). Their geographic distribution is from just north of Cape Hatteras, N.C., to Fort Pierce, Fla. Size range is 4.5 to 5.0 mm; all are females. They were taken in shallow water, 8 to 26 m, on sandy sediments. Little is known about the biology of this species, and the few specimens in the NMFS collection provide no additional information on spawning or length of life.

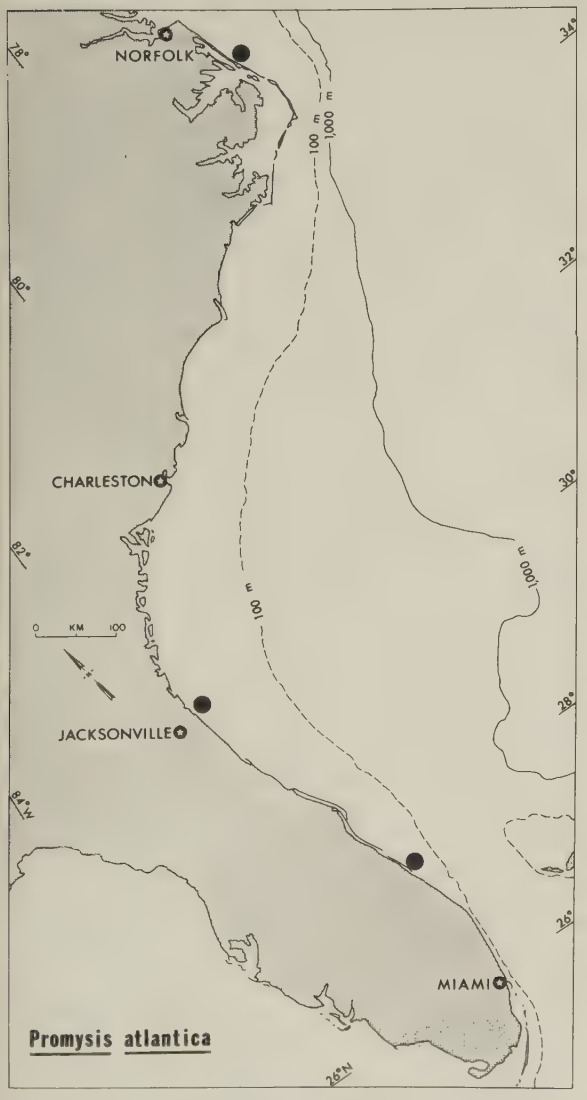

FIGURE 13.—Geographic distribution of *Promysis atlantica* based on specimens in the collection at the NMFS Biological Laboratory, Woods Hole.

Tribe MYSINI

Mysis mixta Lilljeborg, 1852

This boreal mysid occurs in the Eastern Atlantic region from the White Sea, Spitsbergen, Scandinavia and southward to the Baltic Sea, and westward to Iceland. In the Western Atlantic region it has been reported from Greenland, eastern Canada, and the eastern coast of the United States as far south as Cape Cod, Mass. In the Gulf of Maine it has been most frequently reported from off the eastern coast of Massachusetts and from a few localities off the Maine coast (Smith, 1879; Rathbun, 1905; Tattersall, 1951; and others).

This species is represented by 382 specimens from 45 samples in the NMFS collection (Figure 14; Burns and Wigley, Table 15). The majority of specimens, including all adults, were taken in the western part of the Gulf of Maine between Cape Cod, Mass., and the central Maine coast. The first records of this species from south of Cape Cod were collected in the region off Rhode Island and southeastern Long Island, N.Y. The location of the southernmost sample is lat 40°36′ N and long 71°33′ W, approximately 55 km southeast of Montauk Point, N.Y. All 26 specimens from these six southern samples are immatures 10.5 to 20.1 mm in length; they were collected in June and September.

Water depths at all NMFS collecting sites range from 29 to 159 m. Bottom sediments at these localities consist of a variety of types ranging from fine-textured clays to gravel. Most of the samples, however, come from intermediate types of sediment: silt-clay (38%), glacial till (27%), and sand (22%). Only a small percentage of samples represent other bottom types: silt-sand (7%), gravel (4%), and clay (1%).

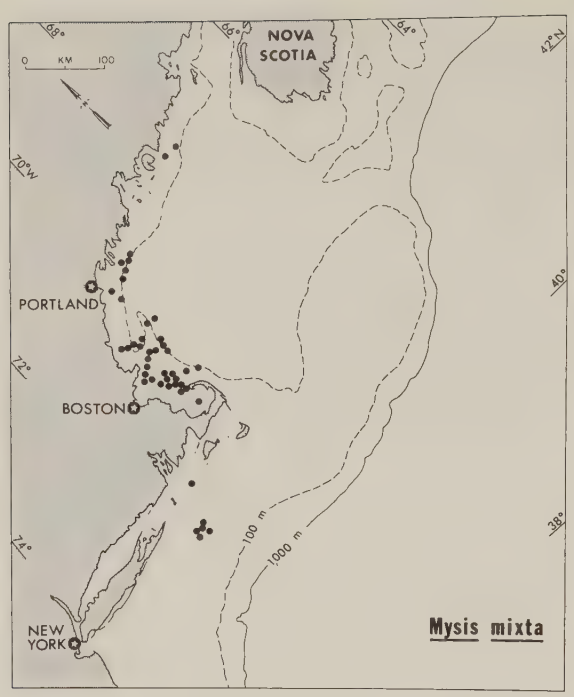

FIGURE 14.—Geographic distribution of *Mysis mixta* based on specimens in the collection at the NMFS Biological Laboratory, Woods Hole.

The occurrence of specimens at the surface (*Albatross IV*, cruise 66-14, station 24) and in several samples between middepths and surface (*Albatross IV*, cruise 66-14, stations 35, 36, 39, and 40), as well as those taken on the sea bottom, indicates a diurnal vertical migration. Specimens at the surface were collected at 0300 hr and midwater samples were taken between 2100 and 0900 hr. This implies inhabitance of upper waters during hours of darkness and a bottom habitat in the daytime.

Sex Ratio

The NMFS collection contains 119 females but only 2 males, which is a ratio of 0.017 male to 1 female. Whether males occur in a habitat different from females, or are actually so much less abundant than females, is unknown. This is the only species in the collection having such a grossly unbalanced sex ratio.

Body Size

Body lengths range from 5.0 to 25.0 mm. Immature specimens are a common component, accounting for 69% of all specimens caught. Many of these immature specimens are large (15 to 20 mm). Also noteworthy is that many large males and females do not possess fully developed secondary sex characteristics. A summary of body length measurements by months and stage of development is listed in Table 7.

TABLE 7.—Means and ranges of body length of *Mysis mixta* by months and stages of development.

Month	Body length			
	Immatures		Adults	
	Mean	Range	Mean	Range
	mm	*mm*	*mm*	*mm*
May	6.9	5.0- 8.5	20.6	19.0-21.3
Jun.	10.5	--	--	--
Aug.	13.6	10.3-20.0	22.0	20.0-24.2
Sept.	18.8	17.2-20.1	--	--
Oct.	16.7	14.0-20.0	23.4	22.0-25.0

Length of Life and Spawning

Although Smith (1879) suggested this species might be an annual that spawns during the winter, our analysis of the maturity status and size frequency data of the NMFS specimens leads us to believe that *M. mixta* has a 2-year life span and spawns in winter or early spring.

Our material is scanty for purposes of determining length of life, but the data do indicate a clear trend in growth and development (Table 7). The specimens reveal two definite age groups in both spring and fall. In May the immatures average 6.9 mm and the adults 20.6 mm. In October the immatures average 16.7 mm and the adults 23.4 mm. Juveniles increase in length at a rate of about 2 mm per month until winter when the growth rate slows appreciably. They mature and spawn in the winter or early spring.

None of the NMFS specimens are ovigerous. The only indication of spawning season is the presence of small (5.3 to 6.3 mm) specimens in May, which suggests a late winter or early spring spawning.

Mysis stenolepis S. I. Smith, 1873

This large American mysid is distributed in coastal waters of northeastern North America from the Gulf of St. Lawrence to New Jersey. Though very common to this region it is represented by only a few specimens in the NMFS collection because biological samples were rarely collected in the intertidal and shallow subtidal zones.

The NMFS collection contains 13 specimens from six samples (Figure 15; Burns and Wigley, Table 16), all from a rather small area off eastern Massachusetts and eastern Rhode Island. The specimens were collected with a dip net along shore in water depths of about 1 m. Four samples were taken in beds of *Zostera* or algae, and one sample was from a sandy bottom (bottom type for the other sample is unknown).

M. stenolepis is one of the largest shallowwater species in the NMFS collection. Body lengths of these specimens range from 13.0 to 26.0 mm, and average 20.4 mm.

FIGURE 15.—Geographic distribution of *Mysis stenolepis* based on specimens in the collection at the NMFS Biological Laboratory, Woods Hole.

According to Smith (1879) the life span of this species is one year. Their life cycle is as follows: (1) adults spawn in winter and early spring, (2) the young appear in late spring and summer, and (3) they mature in the fall and winter. Material in the NMFS collection substantiates this life-cycle plan. Body lengths of specimens, by months, are:

Month collected	Average body length (*mm*)	Stage of maturity
September	14.2	Immature
October	20.0	Mature
November	24.2	Mature
February	25.3	Mature
March	25.0	Mature
April	26.0	Mature

Three larvigerous specimens collected in February and March range in size from 25.0 to 25.5 mm.

Fecundity of this species is very high compared with other east coast mysids. An oviger-ous-larvigerous specimen 25.0 mm long, collected in late February, held 94 eggs and 50 stage III larvae in the brood pouch. Average diameter of the eggs is 0.4 mm and average length of the larvae is 1.4 mm. A 25.5-mm long larvigerous female from the same sample was carrying 188 stage IV larvae; their average length is 1.4 mm. A 25.0-mm larvigerous female collected in March was carrying 171 stage VII larvae; their average length is 1.86 mm.

A rather high water temperature was noted when the September 4, 1961, sample of *M. stenolopis* was collected. The temperature was 23.9° C at a depth of 1 m in an eelgrass bed in Waquoit Bay, Falmouth, Mass. This is the highest temperature recorded for the NMFS samples of this species.

Praunus flexuosus (O. F. Müller, 1776)

This species is very common in shallow coastal waters of Great Britain and along the northern coast of France, Holland, and southern Scandinavia (Tattersall and Tattersall, 1951). In 1960 it was discovered in the harbor at Barnstable,

Mass., (Wigley, 1963) the first report of its occurrence outside the north European area. It has also been collected in large numbers from the coast of New Hampshire by Dr. William F. Black (personal communication), and from the Penobscot River (Maine) estuary by Haefner (1969).

The NMFS collection contains 15 specimens from five samples (Figure 16; Burns and Wigley, Table 17), including four specimens from the original seven taken at Barnstable in 1960.

FIGURE 16.—Geographic distribution of *Praunus flexuosus* based on specimens at the NMFS Biological Laboratory, Woods Hole.

[The other three specimens from this collection were sent to Dr. Olive S. Tattersall, who very kindly examined them and verified the identification (Burns and Wigley, Table 17; footnote 2).] The other samples are also from coastal areas north of Cape Cod, Mass. These were collected along shore at Manomet, Mass.; in the harbor at Nahant, Mass. (by Dr. Nathan W. Riser); at Rye Harbor, N.H. (by Mr. John A. Lindsay); and from a tide pool on Appledore Island, Isle of Shoals, N.H. (by Mr. Stephen Tonjes).

This is a shallowwater species commonly found in tide pools and associated with algae or *Zostera*. All samples in the NMFS collection are from nearshore localities at depths of 5 m or less. The majority of samples were collected by means of a dip net.

Size range of all NMFS specimens is 15.0 to 28.0 mm; males are 15.5 to 19.0 mm and females 16.5 to 28.0 mm. Only three immature specimens, ranging in length from 15.0 to 16.5 mm, are represented in the collection. Sex ratio of the 12 adult specimens is one male to one female.

The spawning season for this species in New England waters, based on the one ovigerous and two larvigerous females in the collection, is at least April through November. It may, however, spawn in this region throughout the year, as it does in Europe. The 25.0-mm female from Barnstable, Mass., held 44 eggs in the brood pouch. The 21.0-mm female from Isle of Shoals, N.H., held 39 stage V larvae in the brood pouch. Although the larvigerous female in the Rye Harbor sample contained 19 larvae, the oostegites were separated and it appeared to be an incomplete clutch.

When this species was discovered in North America in 1960, the question arose whether it was a recent immigrant from Europe, or whether it had inhabited this region for hundreds of years but had been overlooked. After the first capture of only seven specimens most considered it a rare species with only a local distribution in New England. Additional information obtained since 1960, however, indicates it is rather widely distributed between Maine and Cape Cod, Mass., and that it is abundant in the Maine-New Hampshire region. In view of this, and considering the intensive collecting in shallow coastal waters of New England by A. E. Verrill, S. I. Smith, W. Stimpson, and numerous other scientists during the latter half of the nineteenth century, it is our conjecture that *P. flexuosus* is a comparatively new addition to the New England fauna. Possibly it was transported from Europe to a New England port, such as Boston or Portsmouth, N.H., among fouling organisms on the

bottoms of ships during World War II when convoys of merchant ships were making frequent and rather regular transoceanic voyages.

Neomysis americana (S. I. Smith, 1873)

Geographic Distribution

N. americana is the most common mysid inhabiting the northeastern coastal waters of the United States and undoubtedly the most abundant mysid in the western North Atlantic Ocean. It is strictly a North American species, having been reported only from the Gulf of St. Lawrence south to Virginia. It is much more abundant and widely distributed between Virginia and New England than in the northern part of its range.

The NMFS collection originally contained over 2 million specimens of this species—more numerous than any other mysid in the collection, but for purposes of analysis the larger lots were subsampled. Subsamples totaling 8,451 specimens from 168 samples (Figure 17; Burns and Wigley, Table 18) were examined. The geographic distribution of specimens in this collection ranges from off Nova Scotia, near the mouth of the Bay of Fundy, south to Chesapeake Bay.

Most of the specimens are from two regions (Figure 17): (1) eastern Georges Bank to Rhode Island, and (2) from northern New Jersey to Chesapeake Bay. The gap in distribution between these two areas (off Long Island) appears to be more pronounced in offshore waters than inshore. Bigelow and Sears (1939) also encountered a broad hiatus in the occurrence of this species in the offshore waters of eastern Long Island. Yet, inshore in the New York region it has been reported from Great South Bay, Long Island (Smith, 1879) and from Long Island Sound (Verrill, Smith, and Harger, 1873; Smith, 1879; and Richards and Riley, 1967). The only record from offshore Long Island known to us is that reported by Grice and Hart (see footnote 3) which indicated the presence of this species in two plankton samples taken at station 13 located at lat 40°44′ N and long 71°41′ W (water depth, 64 m). The above records indicate merely a restricted occurrence or low abundance in the offshore New York region, not a complete break in distribution.

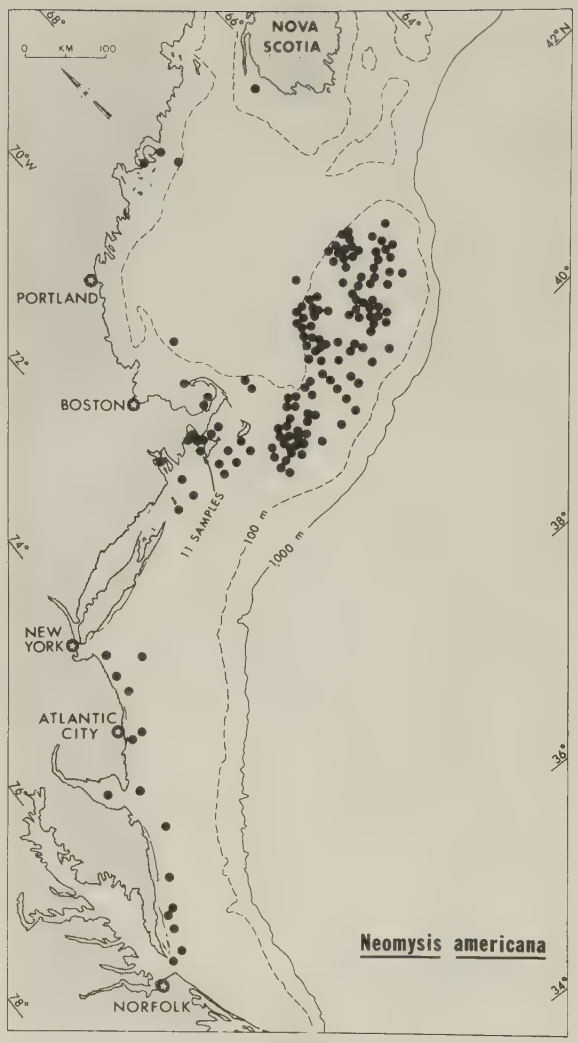

FIGURE 17.—Geographic distribution of *Neomysis americana* based on specimens in the collection at the NMFS Biological Laboratory, Woods Hole.

Samples from the Georges Bank area during summer and winter revealed a similar distribution of *N. americana* in both seasons. The species was present over most of the bank, with highest concentrations in the central part, the same area where Whiteley (1948) also found them to be most abundant.

Bathymetric Distribution

N. americana is a shallowwater species most commonly reported from the intertidal zone to depths of 60 m. However, it appears to inhabit somewhat deeper water in the Georges Bank region as indicated by the records of occurrence in Figure 17. Whiteley (1948) reported it from a number of plankton samples taken at stations where the water depth was 75 m, but at very few localities where depths were greater than 100 m. Greatest depth reported for this species is 214 m (Wigley, 1964).

Depth range for the samples in the NMFS collection is 1 to 232 m. Frequency distribution for these samples is listed in Table 8. This species is common from the intertidal zone out to 90 m but is most abundant at depths between 30 and 60 m.

TABLE 8.—Bathymetric distribution of *Neomysis americana*, based on the NMFS collection.

Water depth	Samples	Specimens
m	*Number*	*Number*
0- 9	5	147
10- 19	14	139
20- 29	20	361
30- 39	19	3,289
40- 49	38	1,998
50- 59	32	1,619
60- 69	13	299
70- 79	12	308
80- 89	4	220
90- 99	2	2
100-109	3	6
150-159	1	3
230-239	1	1
Unclassified	4	59
Total	168	8,451

N. americana undertakes regular vertical migrations between the sea bottom and the upper water layers. Light intensity is the primary controlling element to which the mysids are responding. They move to deeper, darker regions during daytime and upward toward the surface at night (Hurlbut, 1957; Herman, 1963). The NMFS samples provide very little information on this aspect other than to substantiate probable vertical migration in shallow water. At depths of less than 50 m on Georges Bank this species is more common in bottom samples collected during the daytime than at night.

Spawning

Though spawning of coastal populations of *N. americana* takes place throughout the year, it is much more intensive during the warmer months of April through October (Smith, 1879; Fish, 1925; Cowles, 1930; Herman, 1963; Hopkins, 1965). The Georges Bank population was reported by Whiteley (1948) to spawn in the spring. Specimens in the NMFS collection indicate spawning of Georges Bank stocks from March through October and possible spawning in all months of the year. There appear to be two major spawning periods, one in the spring (March through June) and another in the late summer and fall (August through October). Of the ovigerous or largiverous specimens present in samples collected every month from March to October the largest numbers occurred in March through June and August through October. Immature specimens were particularly numerous in August and December. The small number of immature specimens collected in late winter and early spring may indicate occasional small-scale spawning in winter.

Two distinct size groups (summer generation and overwintering generation) of spawning females are discernable; one group spawns in the spring, the other in the fall (Figure 18). Spring spawners have an average length of 11 to 12 mm, and produce a clutch containing about 26 eggs. Fall spawners have an average length of 6 to 8 mm, and their clutch contains only about six eggs. Additional information about these two generations is given below.

Eggs are spherical, 0.38 to 0.42 mm in diameter, in both the summer and overwintering generations.

Size of the larvae varies according to their stage of development. Average lengths in millimeters for the following stages are: stages I and II—0.39, stage III—0.55, stage IV—0.85, stage V—0.96, stage VI—1.15, and stage VII—1.34.

Sex Ratio

The NMFS collection contains 1,574 males and 1,669 females; the ratio is 0.94 male to 1 female.

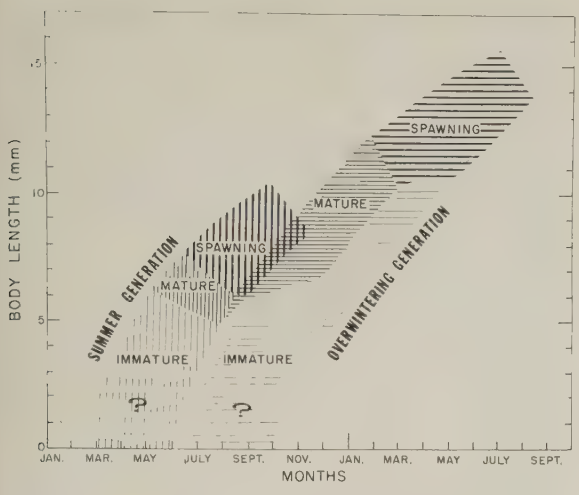

FIGURE 18.—Schematic diagram of the age-size-maturity composition of *Neomysis americana* populations from offshore New England.

Length of Life

The Georges Bank population of *N. americana* appears to consist of two generations: (1) a short-lived summer generation and (2) a long-lived overwintering generation (Table 9, Figure 18). The summer generation stems from eggs that hatch in late winter to late spring. They grow rapidly and mature in late summer and autumn. Length of life of this generation is estimated to be 6 to 10 months. They are the progeny of the overwintering group, the dominant group in the offshore New England area. The overwintering generation originates from eggs that hatch during the summer and autumn, and perhaps even from late spring eggs. They grow at nearly the same rate as the summer generation but do not reach maturity until the following spring. Thus, they are substantially larger than the summer generation. Adults of the overwintering generation are 10 to 15 mm long, compared with 6 to 10 mm lengths for the summer generation adults. Estimated length of life of this overwintering group is 10 to 14 months.

TABLE 9.—Range in body length of the (1) summer and (2) overwintering generations of *Neomysis americana*, by sexes and periods.

Period	Range in length			
	Immatures[1]	Males	Females	
			All specimens	Ovigerous and larvigerous
	mm	*mm*	*mm*	*mm*
Summer generation				
May-June	3.0- 6.8	5.9- 7.4	6.0- 7.4	--
July-Aug.	--	5.0-(9.0)	5.1-(9.0)	6.0- 8.9
Sept.-Oct.	--	5.7-10.0	6.0- 9.6	6.6- 8.3
Overwintering generation				
Sept.-Oct	3.0- 7.0	--	--	--
Nov.-Dec.	3.1- 7.4	5.5- 9.6	5.6- 9.6	--
Jan.-Feb.	8.3-10.5	10.6-12.9	11.5-14.7	--
Mar.-Apr.	6.0-10.9	9.3-12.1	9.3-13.3	10.7-12.4
May-June	--	9.5-14.0	9.5-14.0	11.4-14.0
July-Aug.	--	ca.(9)-13.0	ca.(9)-(14.0)	--

[1] Immatures less than 3 to 4 mm length usually passed through the meshes of the sampling and processing equipment.

Relation to Bottom Sediments

Although *N. americana* make daily excursions from the sea bottom to upper water levels (see Bathymetric Distribution), a substantial amount of their time is spent on bottom, and they appear to be selective in the type of bottom they inhabit. The bottom type with which they are most commonly associated is sand (Table 10). Kinds of sands they inhabit, in decreasing order of importance are: fine, medium, and coarse. One explanation for the scarcity of *N. americana* in the middle and outer shelf areas south of Rhode Island and New York may be unsuitable sediments. The bottom over much of this area is blanketed with silty sands and sandy silt, whereas on Georges Bank and much

TABLE 10.—Frequency of occurrence of *Neomysis americana* in various types of bottom sediments, based on the NMFS collection.

Bottom type	Samples	Specimens
	Number	*Number*
Rock-gravel	5	262
Gravel-sand	10	37
Glacial till	0	0
Shell-sand	4	51
Sand	131	7,987
Silt-sand	7	30
Silt-clay	7	25
Unclassified	4	59
Total	168	8,451

of the nearshore coastal areas where *N. americana* is common, the bottom types are predominantly sands with low silt content (Wigley, 1961; Uchupi, 1963).

Relation to Water Temperature

This mysid is eurythermic and the extremes of temperature in shallow New England waters (0° to over 20° C), in shallow portions of Georges Bank (2°-18° C), and in the vicinity of the Chesapeake Bay (over 25° C), do not appear to inhibit survival of this species. Reproduction and other life processes, however, are affected by temperature. Also, the sequence, timing, or duration of temperature regimes may be important. For example, in the offshore region south of Rhode Island and Long Island, N.Y., where there is a low abundance of this species, the presence of a layer of cold bottom water (the so-called "cold bubble") may have a pronounced influence in repelling immigrants or retarding reproduction.

Tribe HETEROMYSINI

Heteromysis formosa S. I. Smith, 1873

H. formosa is an amphi-Atlantic species that has been reported in the eastern Atlantic from the northern coast of France, British Isles, and Norway. In the western Atlantic it is known to occur along the eastern and southern coasts of the United States from Maine to the Gulf of Mexico. All except three of the western Atlantic records are from the northeastern sector, between Maine and New Jersey. The three southern records are all from relatively deepwater (48 to 227 m) localities. Specimens from 48 m were collected by Brattegard (1969) off Fort Pierce, Fla. The other two records, reported by Tattersall (1951), are based on collections of the research vessel *Albatross* at a depth of 227 m off the coast of North Carolina (lat 34°38′ N, long 75°34′ W) and in eastern Gulf of Mexico (lat 28°36′ N, long 85°34′ W) at a depth of 203 m. (One additional deepwater sample was collected in the northern region by the research vessel *Fish Hawk* at station 917, located south of Martha's Vineyard, Mass., at lat 40°22′ N, long 70°42′ W at a depth of 81 m.)

The NMFS collection contains 72 specimens from 15 samples (Figure 19; Burns and Wigley, Table 19). The geographic distribution of these

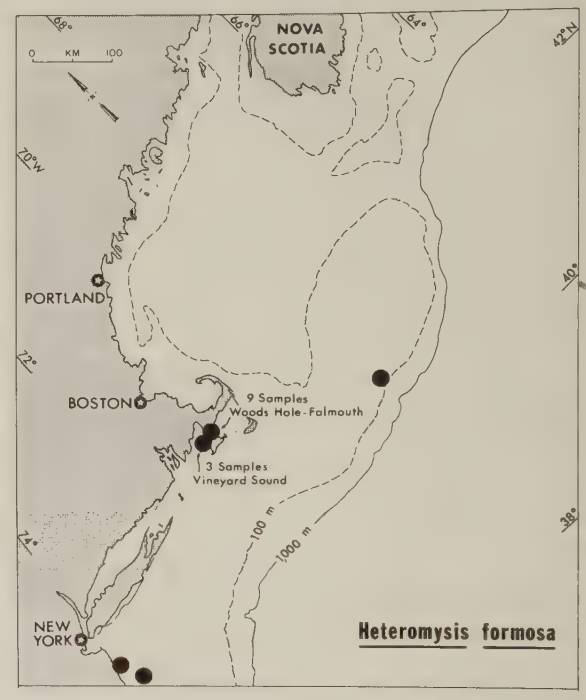

FIGURE 19.—Geographic distribution of *Heteromysis formosa* based on specimens in the collection at the NMFS Biological Laboratory, Woods Hole.

samples extends from southwestern Georges Bank (1 sample) and southern Massachusetts (12 samples) to northern New Jersey (2 samples).

Although the bathymetric range for the NMFS samples is 2 to 84 m, only one sample containing a single specimen was taken at 84 m. All others were collected at depths of 26 m or less. This species customarily inhabits the shallow (1-20 m) inshore areas, such as harbors, bays, and estuaries, where it is much more common than on the outer portion of the continental shelf. The presence of only a single specimen in the NMFS collection from moderately deep water on the outer continental shelf, in contrast to the 71 specimens from inshore locations, illus-

trates the relative scarcity of this species offshore.

Based on NMFS samples, spawning takes place from June to September. Ovigerous or larvigerous females are 5.0 to 8.0 mm long and the number of young per brood is 13 to 15. The average diameter of eggs is 0.4 mm; the length of stage VI larvae is 1.0 mm and of stage VII larvae is 1.7 mm.

The NMFS collection contains 27 males and 31 females, a ratio of 0.9 male to 1 female.

Immature specimens within the size range of 3.4 to 4.5 mm are present in samples from October through January. Body lengths of adults range from 4.7 to 8.9 mm.

This species was collected from a variety of different bottom types (gravel, sand, coarse sand, glacial till, and silty sand). Apparently it has no special affinity for any one kind of sediment, but appears to be more commonly associated with coarse-textured sediments. Members of this species congregate in dead shells of bivalves such as *Mercenaria* and *Spisula*.

Sizes of adult specimens from coastal areas are approximately 5 to 9 mm, whereas the offshore specimens reportedly reach lengths of 15 mm. Owing in part to this difference in size, and partly to their deepwater habitat, Tattersall (1951) considered the possibility that the large offshore specimens collected by the research vessels *Albatross* and *Fish Hawk* might represent a new species closely related to *H. formosa*. He concluded, however, that both groups were similar and only one species was represented.

The deepwater specimen in the NMFS collection is a female only 6.5 mm long. A morphological comparison of this specimen with inshore specimens revealed no major differences that we could detect.

SUMMARY

GENERAL

The principal biological and ecological characteristics for each of the 19 species in the NMFS collection are summarized in abbreviated form in Table 11. This tabulation provides a condensed comparison of one species with another within the NMFS collection and can be used for comparing NMFS information with data from other sources.

TAXONOMIC AFFINITY AND ENDEMISM

The taxonomic affinities of mysids in the NMFS collection are most closely allied with the boreal and subarctic species in the North Atlantic; however, a high degree of endemism is evident.

Nine species having an amphi-Atlantic distribution are: *Eucopia grimaldii, Boreomysis tridens, Erythrops erythrophthalma, Meterythrops robusta, Pseudomma affine, Amblyops abbreviata, Mysis mixta, Praunus flexuosus,* and *Heteromysis formosa.* The eight species that are indigenous to the western North Atlantic are: *Bowmaniella portoricensis, Hypererythrops caribbaea, Pseudomma* sp., *Bathymysis renoculata, Mysidopsis bigelowi, M. furca, Mysis stenolepis,* and *Neomysis americana.* These indigenous species are all inhabitants of warm-temperate to tropical waters. Only one species in the NMFS collection (*Eucopia grimaldii*) is cosmopolitan. Four species (*Eucopia grimaldii, Anchialina typica, Meterythrops robusta,* and *Amblyops abbreviata*) occur in the Pacific Ocean as well as in the western Atlantic. One species (*Promysis atlantica*) occurs in the South Atlantic and North Atlantic Oceans.

GEOGRAPHIC DISTRIBUTION

The geographic distribution of species represented in the NMFS collection differs in scope from single records (of which there are three) to wide-ranging multiple records. *Mysidopsis bigelowi* has the greatest range, extending from northern Georges Bank southward to northern Florida. *Neomysis americana* has a moderate range, extending from northern Gulf of Maine south to Chesapeake Bay. *Bowmaniella portoricensis* and *Promysis atlantica* have widespread ranges in the southern area, with distributions extending from Virginia to Florida. All remaining species were collected within rather limited geographic areas along the eastern coast of the United States, mostly off New England.

TABLE 11.—Summary of biological and ecological information, by species, pertaining only to mysids in the NMFS collection.

Species	Geographic distribution	Bathymetric range	Bottom type	Body length		Spawning season	Number of eggs per clutch[1]
				Range	Smallest adult		
		m		*mm*	*mm*		
Eucopia grimaldii	Slope off southern New England	700	(Silt-clay)	32.0	32.0	--	--
Boreomysis tridens	Slope off southern New England	402	Silt-sand	15.0-26.0	26.0	--	--
Bowmaniella portoricensis	Inner shelf Virginia to Florida	9- 56	Sand	3.1-10.0	6.1	Spring and summer	30
Anchialina typica	Inner shelf South Carolina to northern Florida	32- 38	Sand	4.5- 5.0	4.5	--	--
Erythrops erythrophthalma	Inner and outer shelf and upper slope off New England	18-421	Sand	3.0- 9.6	4.3	(May-Oct.)[2] Aug. and Sept.	15
Meterythrops robusta	Gulf of Maine	64-150	Gravel-sand	6.6-12.0	8.5	(Possibly spring)[2]	--
Hypererythrops caribbaea	Outer shelf off New England	168-179	Sand	5.5-11.0	9.5	Aug.	--
Pseudomma affine	Outer shelf and upper slope off New England	146-329	Silt-sand	4.0-13.1	7.3	July-Dec.[2]	11
Pseudomma sp.	Outer shelf off New England	--	Silt-sand	--	--	--	--
Amblyops abbreviata	Gulf of Maine	183-329	Silt-clay	4.7-15.0	10.0	Dec.	29
Bathymysis renoculata	Slope off southern New England	220-366	Silt-clay	4.0-16.2	13.0	(Possibly spring)[2]	--
Mysidopsis bigelowi	Inner and outer shelf Georges Bank to Florida	13-179	Sand	2.4- 6.6	3.5	(Possibly June-Oct.)[2]	--
Mysidopsis furca	Inner shelf off South Carolina	22	Sand	4.2	4.2	--	--
Promysis atlantica	Inner shelf Virginia to Florida	8- 26	Sand	4.5- 5.0	4.5	--	--
Mysis mixta	Inner shelf off New England	29-159	Various	5.0-25.0	19.0	(Possibly winter or early spring)[2]	--
Mysis stenolepis	Shores of southern Massachusetts and Rhode Island	1	Sand and *Zostera*	13.0-26.0	20.0	Feb. and Mar.	188
Praunus flexuosus	Shores of New Hampshire and eastern Massachusetts	1	Various	15.5-28.0	15.5	Apr.-Nov.	44
Neomysis americana	Inner and outer shelf off New England; inner shelf New Jersey to Virginia	1-232	Sand	3.0-14.7	5.5	Mar.-Oct. (possibly also in winter)	[3]6 [4]26
Heteromysis formosa	Inner and outer shelf Massachusetts to New Jersey	2- 84	Various	3.4- 8.9	4.6	June-Sept.	15

[1] A large proportion of ovigerous females had an incomplete clutch. The values given here refer only to those with a full complement of eggs.
[2] Deduced from the presence of immature specimens at a somewhat later season.
[3] Clutch size of the summer generation.
[4] Clutch size of the overwintering generation.

The presence of 15 species in the New England region (Table 12), compared with only 3 species in the Middle Atlantic and 5 species in the Southern area, is due, in part, to more intensive sampling in the New England waters. However, the recovery of five species in samples from the southeastern coast of the United States where the sampling was sparse, indicates a relatively diverse mysid fauna inhabits that region. Thorough sampling will undoubtedly disclose a number of additional species (new species plus new records for presently recognized species) in all sections of the coast, though the Middle Atlantic region can be expected to contain the fewest species of mysids.

TABLE 12.—Geographic classification of species, based on the NMFS collection.

New England (Nova Scotia south to Hudson Canyon)	Middle Atlantic (Hudson Canyon south to northern Virginia	Southern (Northern Virginia south to Florida)
Eucopia grimaldii		*Bowmaniella portoricensis*
Boreomysis tridens		*Anchialina typica*
Erythrops erythrophthalma		
Meterythrops robusta		
Hypererythrops caribbaea		
Pseudomma affine		
Pseudomma sp.		
Amblyops abbreviata		
Bathymysis renoculata		
Mysidopsis bigelowi	*Mysidopsis bigelowi*	*Mysidopsis bigelowi*
Mysis mixta		*Mysidopsis furca*
Mysis stenolepis		*Promysis atlantica*
Praunus flexuosus		
Neomysis americana	*Neomysis americana*	
Heteromysis formosa	*Heteromysis formosa*	

BATHYMETRIC DISTRIBUTION

The overall bathymetric range at which NMFS mysids were collected is from 1 to 700 m (Table 11). In general all depth zones are rather evenly represented without a preponderance in any one zone. In Table 13 the species are listed under five categories based on the water depths from which they were most frequently caught. Two species were found only in the intertidal zone. Five species are typically

TABLE 13.—Bathymetric classification of species, based on the NMFS collection.

1. Shore Species (occur in the intertidal zone, minimum and maximum depth 0 and 1 m):
   - *Mysis stenolepis*
   - *Praunus flexuosus*
2. Shallow Shelf Species (occur predominantly at depths less than 50 m, minimum and maximum depth 2 and 84 m):
   - *Bowmaniella portoricensis*
   - *Anchialina typica*
   - *Mysidopsis furca*
   - *Promysis atlantica*
   - *Heteromysis formosa*
3. Eurybathic Shelf Species (occur over a broad range of depth on the continental shelf, minimum and maximum depth 1 and 421 m):
   - *Erythrops erythrophthalma*
   - *Meterythrops robusta*
   - *Mysidopsis bigelowi*
   - *Mysis mixta*
   - *Neomysis americana*
   - *Pseudomma* sp.
4. Deep Shelf and Upper Slope Species (occur on the continental slope and outer shelf, minimum and maximum depth 98 and 329 m):
   - *Hypererythrops caribbaea*
   - *Pseudomma affine*
   - *Amblyops abbreviata*
5. Slope Species (occur predominantly on the continental slope, minimum and maximum depth 220 and 700 m):
   - *Eucopia grimaldii*
   - *Boreomysis tridens*
   - *Bathymysis renoculata*

Shallow Shelf (less than 50 m) inhabitants. *Hetermoysis formosa* is included in this category even though one specimen was taken at a depth of 84 m. This is the only New England species in this bathymetric category; all other Shallow Shelf species are warm-water forms collected in the southern region. Six species are listed under the heading "Eurybathic Shelf Species." They were each taken over a broad depth range (for example, *Neomysis americana*, 1-232 m) on the continental shelf and occasionally on the upper continental slope. Three species that live along the outer margin of the continental shelf are listed under the category "Deep Shelf and Upper Slope Species." Depth range for these species is 98 to 329 m. Three species were taken at depths beyond the outer margin of the continental shelf, from 220 to 700 m. They are listed under the category "Slope Species."

SPAWNING

Information pertaining to the spawning seasons of 13 mysid species in the NMFS collection is summarized in Table 11. Direct information based on the capture of ovigerous or larvigerous females is the most convincing evidence; this was obtained for eight species. Additionally, indirect evidence from catch records of immature specimens provides clues to possible spawning seasons of seven species, including four species for which direct evidence is lacking.

Spawning of most species for which information is available takes place during the warmer months—May through October. Species that spawn in this season are: *Bowmaniella portoricensis, Erythrops erythrophthalma, Hypererythrops caribbaea, Pseudomma affine, Amblyops abbreviata, Praunus flexuosus, Neomysis americana, Heteromysis formosa,* and possibly *Bathymysis renoculata* and *Mysidopsis bigelowi.* One species, *Neomysis americana,* probably spawns in all seasons of the year with maximum production in spring. *Amblyops abbreviata* and *Pseudomma affine* spawn in winter and summer; *Meterythrops robusta, Mysis mixta,* and *M. stenolepis* probably spawn in winter or early spring.

The number of eggs or larvae per clutch was counted for eight species. Although the average number per clutch for different species ranges from 6 to 188, these extremes are rare. For most species the average brood contains between 11 and 30; exceptionally small clutches (6 eggs) were produced only by the summer generation of *Neomysis americana.* Unusually large clutches (average of 188 eggs) were typical for one species, *Mysis stenolepis.* A moderately large number of eggs (average of 44) was produced by *Praunus flexuosus.* Both of the latter species are relatively large inshore inhabitants. Small species commonly brood as many eggs as moderately large species; within a species, however, the smaller specimens have fewer eggs than large specimens. The diameter of eggs of ovigerous mysids in the collection was surprisingly uniform. Both large and small species produced eggs that were approximately 0.4 mm in diameter.

BODY SIZE

The smallest and largest specimens (excluding larvae) in the NMFS collection are 2.4 and 32.0 mm in body length. Body lengths were measured for 18 of the 19 species represented

in the collection. (Specimens of *Pseudomma* sp. have not yet been measured.) They have been classified as small, medium, or large. Two criteria were used for determining the appropriate size category: (1) the maximum length of specimens of each species represented in the collection and (2) the length of the smallest adult of each species.

Small species are those with a maximum length of 6.6 mm or less and with the smallest adult 4.5 mm or less. There are four species in this category: *Anchialina typica, Mysidopsis bigelowi, M. furca,* and *Promysis atlantica. Mysidopsis bigelowi* is the smallest species encountered; it matures at a body length of 3.5 mm.

Medium size species are those having a maximum length between 8.9 and 16.2 mm and with the smallest adult 4.6 to 13.0 mm long. There are nine species in this category: *Bowmaniella portoricensis, Erythrops erythrophthalma, Meterythrops robusta, Hypererythrops caribbaea, Pseudomma affine, Amblyops abbreviata, Bathymysis renoculata, Neomysis americana,* and *Heteromysis formosa.*

Large species are those with a maximum length of 25.0 mm or more and with the smallest adult more than 15.0 mm long. There are five species in this category: *Eucopia grimaldii, Boreomysis tridens, Mysis mixta, M. stenolepis,* and *Praunus flexuosus.*

RELATION TO BOTTOM SEDIMENTS

A large majority of mysid species in the NMFS collection live on bottom sediments composed of sand or silty sand. They were least abundant and seldom encountered in gravel and rocky areas. (*Eucopia grimaldii* is excluded from this discussion of mysids in relation to bottom sediments, because it is a bathypelagic species.) Eleven of the 18 benthic species were most commonly associated with sand and silty sand. The sand-dwelling species are: *Bowmaniella portoricensis, Anchialina typica, Erythrops erythrophthalma, Hypererythrops caribbaea, Mysidopsis bigelowi, M. furca, Promysis atlantica,* and *Neomysis americana.* The two most common species are both included with the sand-dwelling inhabitants, but there are significant differences in the habitats they occupy. *Neomysis americana* are occasionally taken on silty sand bottoms, but typically inhabit sand sediments that are silt free or contain very little silt. Conversely, *Erythrops erythrophthalma* have their center of abundance in areas of sand sediments that contain small to moderate quantities of silt. However, the silt content of the sands they occupy is usually insufficient to classify them as silty sands according to the standard classification established by Shepard (1954). Silty sand inhabitants are: *Boreomysis tridens, Pseudomma affine,* and *Pseudomma* sp. The only species that is frequently associated with gravels and other coarse substrates is *Meterythrops robusta.*

Species associated with fine-textured sediments or with various types of bottom materials were usually less abundant and present at fewer localities than the species listed above. Species that were associated with silt-clays are: *Amblyops abbreviata* and *Bathymysis renoculata.* Both species are deepwater inhabitants. Their overall depth range is 183 to 366 m. Fine-grained sediments blanket a large portion of the sea floor at these depths. Species that were found occupying a wide variety of different kinds of bottom sediment types are: *Mysis mixta, Praunus flexuosus,* and *Heteromysis formosa.* These are shallowwater species and the most common bottom types they inhabited were: sand, gravel, silt-clay, glacial till, algae, and eelgrass (*Zostera*).

CO-OCCURRING SPECIES

The catch records reveal a high incidence of co-occurrence of the Atlantic coast mysids. Listed in Table 14 are 15 species, 79% of the total number of species collected, taken in the same sample with one or more other species of mysids. The presence of different species of mysids in dredges, trawls, ring nets, and similar sampling instruments that are towed along the ocean bottom for relatively long distances (hundred meters to several kilometers) reveals a reasonably close spatial occurrence. Unfortunately, the spatial separation between specimens of the different species in such samples prior to

collection are unknown. It was especially interesting to find two species in the same grab sample (Campbell sampler or Smith-McIntyre sampler), for example, *Bowmaniella portoricensis* with *Anchialina typica* or *Mysidopsis furca*. This is good evidence that within an area of 0.48 m^2 of sea bottom *B. portoricensis* lives with *A. typica* or *M. furca*. Also, *Neomysis americana* and *Mysidopsis bigelowi* were caught in the same grab (Smith-McIntyre sampler) samples, but in this case both species were taken from an area of bottom only 0.1 m^2. These examples, of course, do not mean that these species are competitors. They are strong indicators, however, of close habitation and possible competition for space or other living requirements.

TABLE 14.—A list of co-occurring species. Species in column B were present in one or more samples with the corresponding species listed in column A.

A	B
Bowmaniella portoricensis	*Anchialina typica* *Mysidopsis furca*
Anchialina typica	*Bowmaniella portoricensis*
Erythrops erythrophthalma	*Hypererythrops caribbaea* *Pseudomma affine* *Pseudomma* sp. *Mysidopsis bigelowi* *Mysis mixta* *Neomysis americana* *Heteromysis formosa*
Pseudomma affine	*Erythrops erythrophthalma* *Hypererythrops caribbaea* *Amblyops abbreviata*
Pseudomma sp.	*Erythrops erythrophthalma*
Amblyops abbreviata	*Pseudomma affine*
Mysidopsis bigelowi	*Erythrops erythrophthalma* *Hypererythrops caribbaea* *Neomysis americana*
Meterythrops robusta	*Mysis mixta*
Hypererythrops caribbaea	*Erythrops erythrophthalma* *Pseudomma affine*
Mysidopsis furca	*Bowmaniella portoricensis*
Mysis mixta	*Erythrops erythrophthalma* *Meterythrops robusta* *Neomysis americana*
Mysis stenolepis	*Praunus flexuosus*
Praunus flexuosus	*Mysis stenolepis*
Neomysis americana	*Erythrops erythrophthalma* *Hypererythrops caribbaea* *Mysidopsis bigelowi* *Mysis mixta*
Heteromysis formosa	*Erythrops erythrophthalma*

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ESCAPEMENT LEVELS AND PRODUCTIVITY OF THE NUSHAGAK SOCKEYE SALMON RUN FROM 1908 TO 1966[1]

OLE A. MATHISEN[2]

ABSTRACT

Since the inception of a commercial fishery for sockeye salmon in the Nushagak District, Bristol Bay, Alaska, the annual yields have followed a definite pattern. Catches increased during a relatively short development phase of the fishery, then stabilized for some years and then declined in two steps separated by periods of relative stability.

For years the cause of the decline had been thought to be overfishing, and various measures of curtailment had been placed upon the fishing industry.

Evidence is presented in this paper that the average escapement or the potential egg deposition remained about the same during each of three periods (1908-1919, 1925-1945, and 1946-1966); hence the diminution in the runs was due not to lack of spawners but to a decline in the rate of return per spawner.

So that the cause or causes of the present low reproductive potential can be ascertained, the effects of fishing on the stocks of salmon must be examined. Besides removing part of the run, the yearly commercial fishing operation may have altered either the age composition or the distribution of the escapement.

Available historical records were examined for evidence of these types of changes but largely with a negative result; therefore, the hypothesis was advanced that the observed declining rate of return per spawner is caused by a declining basic productivity of the nursery areas. The latter is then ascribable to the cumulative effect of relatively little enrichment of bioenergetic elements from salmon carcasses since the instigation of commercial fishing operations in comparison with the prefishing era when the entire virgin run escaped to the spawning grounds.

Suggestions are made for future field testing of this hypothesis.

In the development of the salmon fishery along the eastern perimeter of the Pacific Ocean, the most southern stocks were utilized first. As demand increased and certain stocks declined, the fishery shifted northward until the runs of the entire southeastern Alaska and soon thereafter those of the western districts were exploited. The rapidity of growth of the salmon fishing industry in Alaska is astonishing. The first cannery was built in southeastern Alaska at Klawak in 1878 (Rich and Ball, 1928), and only 6 years later exploratory fishing was conducted in Bristol Bay.

The early Bristol Bay catch records show that, from 1884 to 1891, fishing was conducted only in Nushagak Bay (Figure 1). Four years later, salmon was harvested in the other watersheds of Bristol Bay, the Kvichak-Naknek, the Egegik, and the Ugashik Districts. The patterns were initially alike, with a continuous and steady rise in production for at least 10 years in the smaller districts of Egegik and Ugashik and 20 years or more in the Nushagak District and even longer in the Kvichak District where on the average more than 60% of the Bristol Bay harvest is made annually.

As these four fisheries developed, annual variations became more and more apparent, but the overall production was fairly stable until 1919, when it declined drastically all over Bristol Bay in spite of no decline in fishing effort. The catches in Ugashik, Egegik, and Kvichak Districts soon thereafter rebounded to their former production level, but the catches in the Nushagak District did not. From this point on, the pattern of development in Nushagak differed from that of the other fishing areas in Bristol Bay, primarily in a more severe and persistent decline of the stocks making up the entire run.

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In an effort to reverse this downward trend by providing for larger escapements, fishing effort was reduced by restrictions on fishing time, gear, and location. The effect of these measures can be gauged from three principal sources of information: (1) A counting weir was operated in the Wood River of the Nushagak District, the principal trunk stream, during the years 1908-1919. (2) Biological studies were conducted in subsequent years that provided data on the age, length, and size composition of the catch and in part of the escapement. (3) The salmon canning industry itself has kept meticulous records on daily catches, number of fishing units, and type of gear operated.

The various sources of data indicated above were utilized to reconstruct the levels of escapements in the Nushagak District during the last 50 years in an effort to determine whether the magnitude of the yearly escapements is correlated with the declining salmon production in Nushagak Bay. If this were not the case, the fishery may have changed the age and size composition of the stock or the distribution of the various stocks in time and space. These factors will be examined in a search for a logical explanation of the decline of the Nushagak fishery.

NUSHAGAK BAY AND WATERSHED

Nushagak Bay includes the waters between a line drawn from Nichol's Spit to Etolin Point and the confluence of the Wood and Nushagak Rivers (Figure 1). These streams serve as the trunk streams of the Wood River lakes and the Tikchik lakes, respectively. Two other trunk streams drain into Nushagak Bay, namely, the Snake River and the Igushik River. The entire watershed comprises a drainage basin of 10,207 km^2. The morphometric parameters of some of the more important salmon-producing lakes are given by Gadau (1966).

Although sockeye salmon occur in more northerly latitudes, the Nushagak River system represents the northern boundaries of large sockeye salmon runs. The reason may be the absence of large lakes in more northern stream systems, which would provide sufficient nursery grounds. Thus, in the Tikchik system there are six lakes with five accessible to the salmon, but only the three lower ones, indicated on Figure 1, are important for sockeye salmon production.

NUSHAGAK SOCKEYE CATCHES, 1884-1966

The commercial fishery for sockeye salmon in Bristol Bay began in Nushagak Bay in 1884 after the schooner *Neptune* made an exploratory salting expedition (Moser, 1902). Prior to that time, some salting, from 800 to 1200 barrels each year, was done by fishermen operating a simple trap in the Wood River.

The most recent account of catch data was published by Kasahara (1963). His figures differ in some years from those given in Tables 1 and 2 of this paper, compiled in part from original sources, but the discrepancies are mostly minor in nature, and they do not change the overall picture in catch level and trend. Derivation of the Nushagak catch figures used in this report is given in the footnotes and comments to the mentioned tables.

When the Nushagak catches are plotted, they exhibit strong annual variations, as in most sockeye salmon runs (Figure 2). A small part of the variability can be explained by differences in fishing effort, which reflected economic conditions or inaccurate predictions by the cannery superintendents as to the actual size of the run. Viewed over longer time periods, however, there can be no doubt that the annual catches reflect changes in stock strength. This conclusion is amply brought out by the construction of a trend line by a moving average of 5's because of 5-year cycle.

Three distinct periods are discernible. The first period spans the years 1900-1918, the second one covers the years 1921-1945, and the last period includes the years 1946-1966. The average annual catches during these periods were 5,134,156; 2,888,726; and 1,183,485 salmon, respectively.[3]

Transition from one level to the next took

[3] If the estimated foreign catches made since 1956 were included with the domestic catches for the third period, the average annual catch would be raised about 25%.

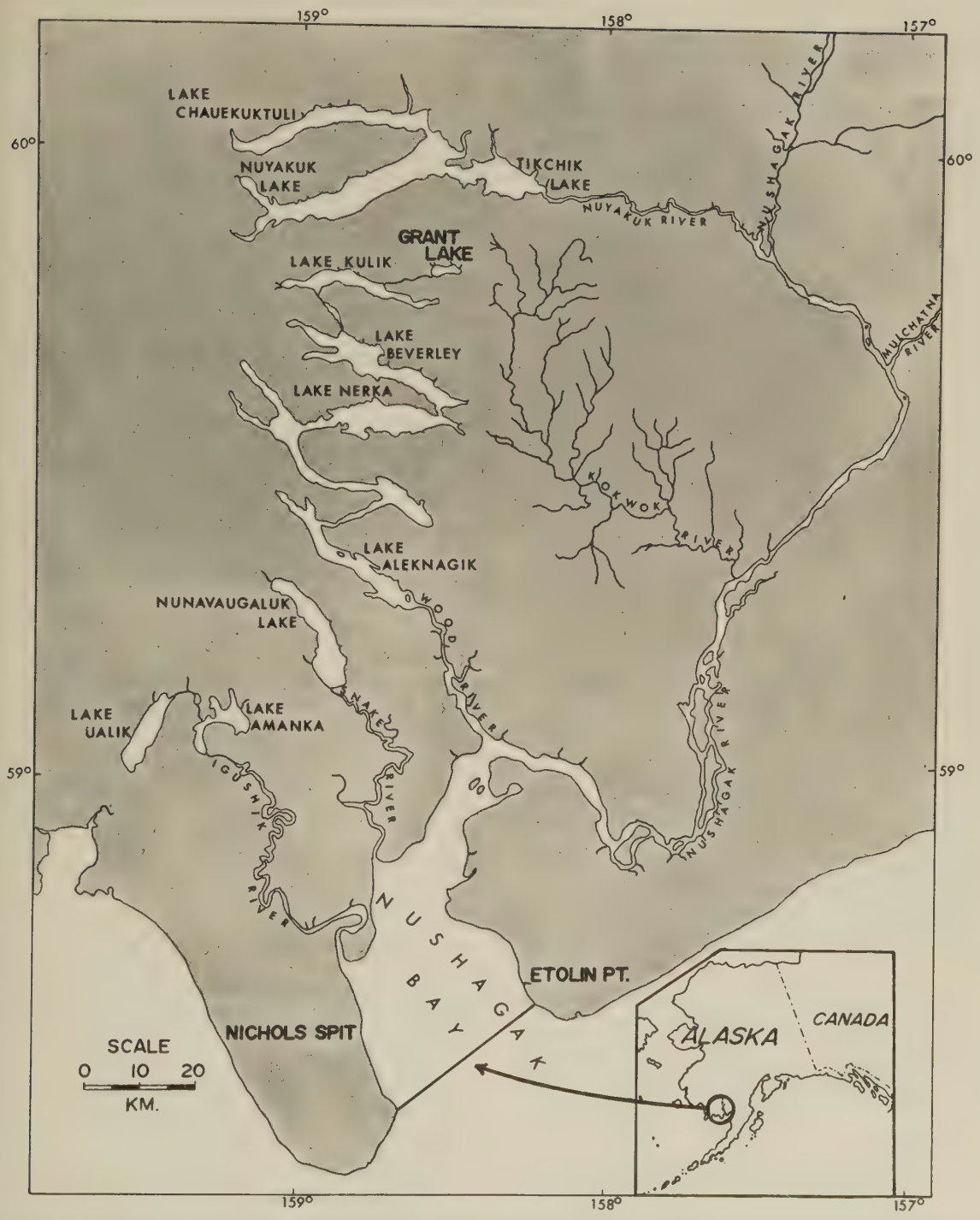

FIGURE 1.—The Nushagak District of Alaska showing (from north to south) the Tikchik, Wood River, Snake River, and Igushik River lake systems.

TABLE 1.—Commercial catches of sockeye salmon, Nushagak Bay, 1893-1945.

Year	Number of fish	Year	Number of fish
1893	640,000	1921	3,717,284
1894	860,000	1922	3,408,358
1895	938,946	1923	1,921,874
		1924	2,168,154
1896	1,262,690	1925	3,903,125
1897	1,240,080		
1898	1,890,092	1926	4,022,328
1899	2,517,436	1927	657,467
1900	4,234,533	1928	4,957,096
		1929	3,851,479
1901	5,401,051	1930	1,610,568
1902	4,725,715		
1903	6,319,189	1931	2,260,541
1904	5,345,659	1932	3,083,615
1905	7,387,935	1933	3,753,230
		1934	4,575,049
1906	5,427,512	1935	649,093
1907	2,627,351		
1908	6,092,031	1936	1,560,138
1909	4,906,635	1937	4,561,298
1910	4,469,755	1938	2,322,704
		1939	4,169,121
1911	2,957,073	1940	1,519,082
1912	3,993,428		
1913	5,409,933	1941	1,897,869
1914	6,457,815	1942	2,465,779
1915	5,904,862	1943	3,373,643
		1944	3,513,241
1916	3,744,551	1945	2,296,019
1917	5,847,239		
1918	6,296,702		
1919	1,477,336		
1920	2,682,056		

Sources:
1884-1927 — Rich and Ball (1928).
1929-1945 — Annual District Management Reports, District Agents. Bureau of Fisheries and Fish and Wildlife Service.

Comments:
The catches for 1884-1892 are only given in cases and therefore are not included.
For the years 1925-1946, Alaska Salmon Industry gathered data on the catch, the pack, and expended effort by the major fishing companies.
The number of fish per case is computed from the information collected by Alaska Salmon Industry. It was used for conversion of the case pack into number of fish for the years 1929, 1930, 1931, 1932, and 1941, since only the case pack is recorded for these years in the Reports of the Management Agencies.
One 200-lb. barrel of salted salmon has been set equal to 54 fish and one 350-lb. barrel equal to 95 salmon.
The official records for the year 1928 list only canneries that operated in Nushagak in this year. The catch figure used is based on records submitted to Alaska Salmon Industry from all but two canneries. The catch in the latter case was extracted from the sworn reports submitted by the fishing industry to the tax authorities.

place within 2 to 3 years. Although the other districts in the Bristol Bay region have experienced a decline in production, this decline has been neither so distinct nor so drastic in nature as in the Nushagak District.

FISHING GEAR AND AREAS IN NUSHAGAK BAY

Three types of fishing gear have been utilized in Nushagak Bay—traps, drift gill nets, and

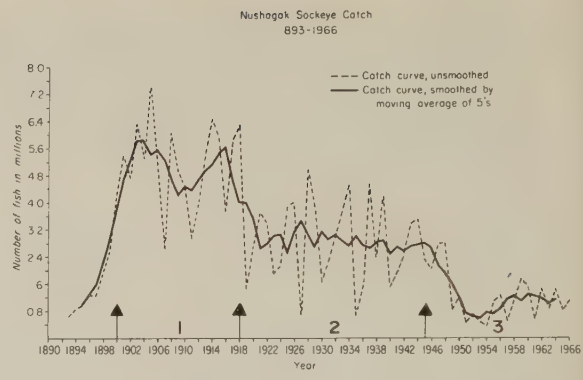

FIGURE 2.—Catches of sockeye salmon in the Nushagak fishery, 1893-1966.

stationary gill nets (set nets). Traps were not used to any great extent in the Nushagak fishery or in Bristol Bay as compared with other areas of Alaska, in which they were in widespread use. The main factor which discouraged the use of traps undoubtedly was the strong tidal currents in Bristol Bay, where tidal differences reach as high as 25 ft or more and peak water velocities reach 4 to 5 knots. These conditions permitted trap operations only in a restricted number of places. Since gear records became available in 1904 and until traps were outlawed in 1923, their number in Nushagak Bay varied from 3 to 11 (Rich and Ball, 1928).

Apparently set nets were not commonly used during the period when traps were legal. The first documented set net catches were taken in 1924, and set nets are mentioned in the 1926 regulations. A maximum length of 75 fm was set in 1926, but in 1931 maximum length was reduced to 50 fm, as is the case today. Since the advent of yearly reports by the management agent in 1929, accurate records have existed as to the distribution of effort between these two types of gear.

Up to and including 1922, no restrictions were placed on mesh size and length of the drift gill nets. In 1924, the maximum length of drift nets was set at 200 fm and mesh size of at least 5¾ inches, stretched measure, between knots. After the 1925 season, minimum size was set at 5½ inches. No other changes in mesh regulations

TABLE 2.—Catches and escapements of sockeye salmon in Nushagak District, 1946-1966.

Year	Catch	Escapement by river system			Estimated total run	Escapement as percent of total run
		Wood River	Other streams	Total		
1946	2,028,144	3,717,000	1,002,000	4,719,000	6,747,144	70.0
1947	2,767,287	1,782,000	725,000	2,507,000	5,274,287	47.5
1948	2,805,793	1,483,250	608,000	2,091,250	4,897,043	42.7
1949	800,123	101,025	37,000	138,025	938,148	14.7
1950	1,212,091	451,600	121,000	572,600	1,784,691	32.1
1951	436,950	457,600	82,000	539,600	976,550	55.3
1952	698,071	226,800	207,000	433,800	1,131,871	38.3
1953	449,341	515,542	313,000	828,542	1,277,883	64.8
1954	315,357	570,624	121,000	691,624	1,006,981	68.7
1955	1,054,978	1,382,755	551,000	1,933,755	2,988,733	64.7
1956	1,263,186	773,101	439,000	1,212,101	2,475,287	49.0
1957	491,498	288,727	210,000	498,727	990,225	50.4
1958	1,092,156	960,455	317,478	1,277,933	2,370,089	53.9
1959	1,719,687	2,209,266	832,619	3,041,885	4,761,572	63.9
1960	1,517,988	1,016,073	657,185	1,673,258	3,191,246	52.4
1961	511,483	460,737	398,896	859,633	1,371,116	62.7
1962	1,461,766	873,888	63,810	937,698	2,399,464	39.1
1963	842,744	721,404	342,452	1,063,856	1,906,600	55.8
1964	1,420,941	1,076,112	262,892	1,339,004	2,759,945	48.5
1965	793,323	675,156	424,110	1,099,266	1,892,589	58.1
1966	1,170,271	1,208,682	422,044	1,630,726	2,800,997	58.2
Total	24,853,178	20,951,797	8,137,486	29,089,283	53,942,421	--
Average 1946-1966	1,183,485	997,705	387,499	1,385,204	2,568,689	51.9

Sources:
1946-1959 — Mathisen, Burgner, and Koo (1963).
1960-1966 — Alaska Department of Fish and Game, Division of Commercial Fisheries, Bristol Bay Area, Annual Management Report 1966, 59 p.

were made until 1961, when 5⅜-inch nets were permitted.

The length of drift nets was reduced to 150 fm per boat in 1929 and has remained unchanged. However, the industry did not necessarily always feel compelled to observe these maximum and minimum limits. The gill net fishery developed before such regulations were introduced and enforced. The necessity of observing a correspondence between the pull of the boat and the drag of the gill net had more or less standardized the gear. Length of the drift net and mesh size as actually used can be studied from two other sources (Table 3).

For the period 1902-1925, the mesh sizes and lengths of the drift nets used were given in the yearly reports of two canneries belonging to Alaska Packers Association in Nushagak.

Since 1926 reports have been submitted by the operators to the Federal government concerning their canning activities. These sworn statements give the lengths of nets used by the different companies. Since the advent of statehood, gear regulations have been published annually.

There has been a gradual but steady decline of the mesh size to 5⅜ inches, stretched mesh. In contrast, the length of the drift nets has been remarkably constant. Even when an upper limit of 200 fm was introduced in 1924, many opertors used nets half this size or 100 fm. Since 1928, all drift nets have measured 150 fm long,

TABLE 3.—Mesh sizes and lengths of drift gill nets used in the Nushagak sockeye salmon fishery, 1902-1966.[a]

Year	Stretched mesh size	Length of drift net
	inches	*fathoms*
1902	6⅛-6¼	--
1903	6⅛	120
1904	6-6⅛	150
1905	6⅛	150
1906	6-6⅛	150
1907	6 1/16-6¼	160
1908-1912	6	160
1913-1925	5¾	150b
1926-1927	5½-5¾	100-200c
1928-1960	5½	150d, e
1961-1966	5⅜	150

a Information prior to 1925 taken from records of the Alaska Packers Association and for subsequent years from announced regulations of the Federal Authorities.
b A maximum legal length of 200 fm and minimum mesh size of 5¾ inches specified for 1924 and 1925.
c A minimum mesh size of 5½ inches set for new nets.
d A maximum length 150 fm set in 1929.
e A maximum length of 100 fm set for 1937 only.

except for the year 1937, when the maximum size was reduced to 100 fm for 1 year and only for Nushagak Bay.

Powered fishing boats were outlawed in 1922 and not permitted again until 1951. However, in the 30's the canning companies started to use small tug boats to tow the fish boats from one place to another, or most commonly to assist in bringing a boat to the delivery scow. Consequently, the efficiency of one boat increased with this added mobility. In part, it was offset by the movement of fishing boundaries over the years farther and farther out from the river mouth and thereby reduction in efficiency of the fishing gear.

In 1899, fishing above tidewater was prohibited in streams less than 500 ft in width. In the tidewater of smaller streams, gear could only cover one-third of the stream width.

In 1907, fishing in the Wood and Nushagak Rivers was prohibited within 500 yards of the mouth of Wood River. Over the years, gradually, restrictions of fishing area have been imposed, which resulted in a transfer of fishing operations away from the river and river mouth and into the open Nushagak Bay. In Figure 3 are indicated locations of canneries in operation shortly after the turn of the century. Only three plants remain actively canning in Nushagak Bay today.

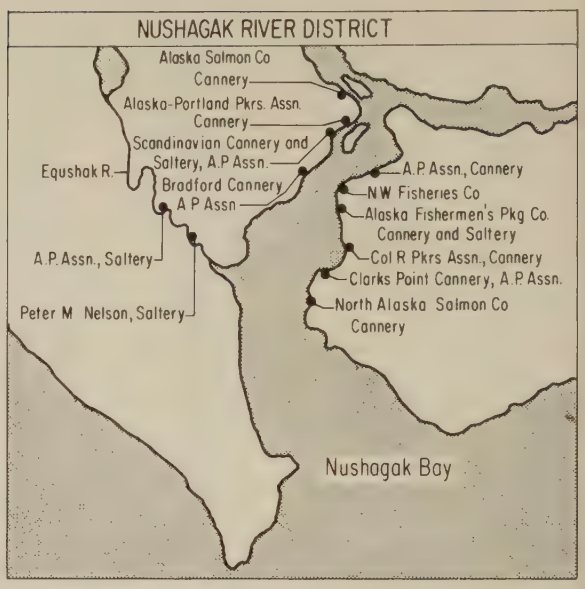

FIGURE 3.—Copy of an old map (probable date 1907) with the locations of canneries and salteries in Nushagak Bay. Canneries in operation today are the Columbia-Wards Cannery at the site of North Alaska Salmon Company Cannery, a Queen Fisheries plant near Columbia River Packers Association plant, and Pacific Alaska Fisheries Dillingham plant at the site of Alaska-Portland Packers Association.

THE NATURE OF THE SOCKEYE SALMON RUNS

All sockeye salmon runs to Bristol Bay have a very distinct and regular time schedule. Historically, the period from June 25 to July 25 has been considered as the time when the salmon are present in Nushagak Bay in catchable quantities. Records accumulated since 1955 indicate that, on the average, peak catches in Nushagak Bay were made on July 5 (Royce, 1965).

The entry is of a pulse type with exponential declining departure curves for the trunk streams and the spawning grounds (Mathisen, 1969). Bi- or trimodal catch curves, especially in earlier years, undoubtedly were created by changes in frequency or relative strength of the individual pulses. We do not know the racial composition of the individual pulses, but some tagging data (Straty, 1969) point to a fairly random mixing of individual races.

Basically, the juvenile salmon spend 1 or 2 years after emergence in the nursery areas of the freshwater lakes. They return from ocean feeding after 2 or 3 years. Thus, four different age groups will make up a year's run, namely, 1.2, 1.3, 2.2, and 2.3 (after Koo's [1962] notation). The number of fish in other age groups is insignificant and can be disregarded. The Nushagak District differs from other districts in Bristol Bay in having a preponderance of 1-freshwater check salmon.

ESCAPEMENT LEVELS IN THE NUSHAGAK DISTRICT

The history of the Nushagak fishery was divided earlier into three periods. Within each of these periods data exist in regard to escape-

ment levels, although they differ in completeness. Naturally the best records have been assembled during the last period, while the most incomplete records exist from the middle period. The escapement records are discussed in order of completeness.

THE PERIOD 1946-1966

The records for this period are complete in the sense that escapement estimates were made for all streams draining into Nushagak Bay (Table 2). Estimates were based originally on ground or aerial surveys. In 1953, the Wood River escapement was estimated from tower counts in the trunk stream. In 1958, this technique was adopted for assessment of the Igushik escapement, and in 1959 for that of the Nuyakuk River. From 1960 to 1964, tower counting was conducted in the Snake River system and inaugurated in the Nushagak-Mulchatna River in 1966. Otherwise, escapement estimates were made by the less reliable aerial survey. The earlier estimates based on ground surveys all have in common a much larger variance, but they gain in consistency because of the fact that largely the same personnel conducted spawning surveys in all years, even after introduction of tower counts (Gilbert, 1968).

In the present context, we are not primarily interested in the year-by-year changes in catch and escapement level, rather in the overall ratio of catch to escapement over the entire period. The average catch amounted to 1,183,485 sockeye salmon and the average escapement to 1,385,204 spawners. The ratio is almost one to one; or on the average, a pair of spawners produced a progeny of four fish. In terms of fishing mortality, the rate of exploitation has averaged 48.1%.

THE PERIOD 1908-1919

No total escapement estimates exist for this period, except for the Wood River system where a counting weir was operated from 1908 to 1919 with the exception of the 1914 season. Daily counts and comments on weir building and maintenance are found in Reports of the Commissioner of Fisheries for the years in question (Table 4).

On the assumption that the ratio of the Wood River escapement to the total Nushagak escapement was the same for the years 1908-1919 as was observed during the period 1946-1966, when estimates were available of the Wood River escapement as well as of the total Nushagak escapement, then this ratio can be used to estimate the total Nushagak escapement for the years 1908-1919 from the weir counts.

The ratio of the total Nushagak escapement to the Wood River escapement has been computed in two ways from data in Table 2. The first ratio

TABLE 4.—Total Nushagak escapement 1908-1919.

Year	Wood River weir count	Estimated Nushagak escapement	Catch	Estimated total run	Escapement as percent of total run
1908	2,603,655	3,758,636	6,092,031	9,850,667	38.2
1909	893,244	1,289,487	4,906,635	6,196,122	20.8
1910	670,104	967,362	4,469,755	5,437,117	17.8
1911	354,299	511,466	2,957,073	3,468,539	14.7
1912	325,264	469,551	3,993,428	4,462,979	10.5
1913	753,109	1,087,188	5,409,933	6,497,121	16.7
1914	No count	--	6,457,815	--	--
1915	259,341	374,385	5,904,862	6,279,247	6.0
1916	551,959	796,808	3,744,551	4,541,359	17.5
1917	1,081,508	1,561,265	5,847,239	7,408,504	21.1
1918	943,202	1,361,606	6,296,702	7,658,308	17.8
1919	145,114	209,487	1,477,336	1,686,823	12.4
Total	8,580,799	12,387,241	57,557,360	63,486,786	--
Average 1908-1919	780,073	1,126,113	4,796,447	5,771,526	19.5

Sources: Reports of the Commissioner of Fisheries for the fiscal years 1908 through 1919 and special papers. Government Printing Office, Washington, D.C., 1910-1921.

is based on the data for the years 1946-1957, when the escapement estimates were made largely from ground and aerial surveys. Presumably this estimate is less reliable than the second estimate based on the years 1958-1966, when the escapement estimates were based largely on very reliable tower counts. The two ratios are 1.4438 and 1.4433.

Thus the average Wood River escapement has formed a remarkably constant proportion of the total Nushagak escapement regardless of which years are used for calculation. Consequently, the ratio 1.4436, based on data for all the years 1946-1966, has been used to enlarge the early Wood River weir counts from 1908 to 1919 to reflect the Nushagak escapement for the same years.

Estimated in this manner, the annual Nushagak escapement for the period 1908-1919 averaged 1,126,113 spawners, and the total Nushagak sockeye run averaged 5,771,526 salmon, or a rate of exploitation of 80.5%.

THE PERIOD 1925-1945

No weir counts exist for these years, and quantitative stream surveys were not conducted. However, escapement estimates can be made from available data on the catch, size distribution of the fish, sex ratio, and expended effort.

From 1926 on, the legal minimum mesh size was 5½ inches, and from 1927 the maximum length of the drift gill nets remained unaltered at 150 fm. An exception must be made for 1937, when the maximum length was reduced to 100 fm for this one year in the Nushagak fishery. Therefore, given a measure of the catch and the instantaneous rate of fishing for each centimeter group by the 5½-inch gill nets and an estimate of expended fishing effort, the escapement can be calculated by centimeter groups from the formula for competitive fishing units and summed over the size range observed in a year to give the total escapement:

$$E = \sum_{j=a}^{b} C_j \frac{1}{e^{fq_j} - 1},$$

where E = the unknown total escapement,
C_j = the known catch for size group j,
q_j = the coefficient of catchability for size group j,
f = the number of standardized fishing units, and
a and b = lower and upper bounds of the size range.

No natural mortality has been assumed during the fishing season.

Because of the different selection curves for males and females by 5½-inch mesh size, these calculations must be done separately for each sex. The necessary data for this calculation follow.

Sex Ratios

It has been assumed that no selection for sex was exerted in the collection of samples for size and age composition. Consequently, the numbers of males and females measured in a day provide an estimate of the sex ratio in the catch for that particular day. This procedure was necessitated by the absence of specific sex ratio samples.

Size Composition of the Catch

During the years considered here, the Bureau of Fisheries stationed biologists at selected canneries for collection of scale samples and length measurements. At other times, resident people were hired for the same purpose and paid a fixed amount for each scale book collected.

Generally the type of length measurements made is not indicated in the records; but it has been assumed that the procedure was to measure length from the tip of the snout to the fork of the tail. This assumption was verified by a comparison of the resulting length-frequency curves with the mean lengths of 2- and 3-ocean fish in postwar years.

Since 1946, the common procedure has been to measure the length of the sockeye salmon taken in the fishery from the middle of the eye to the fork of the tail. The Fisheries Research Institute took a series of double measurements in 1946 to provide a basis for constructing a regression line between the two types of measurements, and a conversion can be made from one

measurement to the other by means of the two following equations:

$$\delta : \text{ME-TF} = 536.772 + 0.8279\,[(\text{snout-TF}) - 592.340]$$

$$♀ : \text{ME-TF} = 527.481 + 0.8946\,[(\text{snout-TF}) - 569.724]$$

Commonly, length measurements were collected throughout the fishing season. These measurements were grouped by fishing periods or by time periods for which catch records exist. Finally, a seasonal weighted length-frequency distribution was computed by the use of the period catches as weighting factors.

Expended Fishing Effort

Batts and Fischler (1967) have summarized the fishing regulations promulgated during the years 1924-1945. A summary of the allowable fishing time is given in Table 5, without consideration for the stage of the tide in relation to closed and open periods. Although the largest or smallest tides generally are inferior fishing periods compared with the medium-sized ones, no correction was attempted on the premise that the plus and minus deviations tended to cancel each other over the entire season.

The number of fishing boats that operated each year for the period 1929-1945 is recorded by the management agents in their annual reports and copied in Table 5. The size of the Nushagak fishing fleet in 1925-1928 was estimated from the data collected by the Alaska Salmon Industry. More than 60% of the total Nushagak catches during these 4 years were made by the reporting canneries, which also submitted records on the number of boats employed. By direct proportionality an estimate was derived for the total number of fishing boats and set nets that operated from 1925 to 1929 (Table 5).

So that a common unit of effort could be derived, the fishing power of set nets was expressed in terms of that for drift nets according to a method by Robson (1961).[4] The conversion was made separately for each year by consideration

[4] Robson, D. S. 1961. Estimation of the relative fishing power of individual ships. Cornell Univ., Biometrics Unit, Plant Breeding Dep., BU-133-M. (Unpublished manuscript.)

TABLE 5.—Registered fishing effort in Nushagak Bay, Bristol Bay, Alaska, 1925-1950.

Year	Total fishing time in days	Total number boats (drift nets)	Total boat day units	Total number set nets	Total set net day units	Relative efficiency set nets/boats	Set net units converted to boat units	Total effort in boat days
1925	22.000	337	7,414	66	1,452	.0717	104.0	7,518
1926	21.000	256	5,376	44	924	.1153	106.5	5,483
1927	19.500	292	5,694	68	1,326	.2796	370.7	6,065
1928	22.500	264	5,940	39	878	.3288	288.7	6,229
1929	21.000	311	6,531	115	2,415	.3613	872.5	7,404
1930	15.250	335	5,109	112	1,708	.1640	280.1	5,389
1931	13.500	351	4,739	152	2,052	.3264	669.8	5,409
1932	18.333	276	5,060	208	3,813	.1151	438.9	5,499
1933	18.688	280	5,233	167	3,121	.1617	504.7	5,738
1934	19.666	279	5,487	221	4,346	.0833	362.0	5,849
1935	9.000	65	585	154	1,386	.2981	413.2	998
1936	17.750	298	5,290	263	4,668	.5129	2,394.2	7,684
1937	19.500	236	4,602	173	3,374	.1594	537.8	5,140
1938	19.500	99	1,931	96	1,872	.2426	454.1	2,385
1939	19.000	235	4,465	144	2,736	.3217	880.2	5,345
1940	14.000	129	1,806	128	1,792	.5773	1,034.5	2,841
1941	19.000	125	2,375	116	2,204	.1803	397.4	2,772
1942	27.500	96	2,640	53	1,458	.2827	412.2	3,052
1943	21.500	119	2,559	98	2,107	.3850	811.2	3,370
1944	24.000	118	2,832	103	2,472	.2889	714.2	3,546
1945	20.000	82	1,640	164	3,280	.2134	700.0	2,340
1946	16.500	198	3,267	119	1,964	.3077	604.3	3,871
1947	21.000	181	3,801	190	3,990	.2650	1,057.4	4,858
1948	16.000	198	3,168	216	3,456	.4709	1,627.4	4,795
1949	10.400	192	1,997	272	2,829	.2255	637.9	2,635
1950	13.500	108	1,458	270	3,645	.1728	629.9	2,088

of 5 days during the peak of the fishing season. This procedure eliminated some of the variability present at the beginning or the end of the fishing season due to irregular entries or departures of the salmon. The choice of 5 days was made in order to avoid too complicated a scheme, and often more than half of the total Nushagak catch was taken during the time period considered.

In this two-way classification with two rows corresponding to drift net and set net and five columns corresponding to the time periods, the catch in 1 day and by a given type of gear is:

$$C_{ij} = f_{ij} \cdot r_i \cdot N_j \cdot \epsilon_{ij} ,$$

where f_{ij} = the number of fishing units of type i operated on day j,
r_i = the coefficient of catchability of gear type i for all size groups,
N_j = the average stock of salmon encountered by the gear on day j, and
ϵ_{ij} = error term.

If $r..$ is the coefficient of catchability of a unit of a theoretical average of all types of gear, one can write $\alpha_i = r_i/r..$ Similarly, if the average stock size encountered by the gear during the entire period is defined as $N..$, one has $\beta_j = N_j/N..$ Finally, the error term was considered log-normal (Beverton and Holt, 1957).

The random variable $Y_{ij} = \log (C_{ij}/f_{ij})$ can be written then as

$$Y_{ij} = m + a_i + b_j + e_{ij}.$$

Since we have only two types of gear, $\log r_2 - \log r_1 = a_2 - a_1$. An estimate of a_1 can be obtained directly from a linear hypothesis program, such as BMD 05V (Dixon, 1965), under the constraint $a_1 + a_2 = 0$. The results expressed as arithmetic ratios are listed in Table 5.

Fishing Power of 5½-Inch Gill Nets

Two size groups of fish predominate in all Bristol Bay sockeye salmon fisheries (Mathisen, Burgner, and Koo, 1963). The 3-ocean fish measure on the average from 5 to 6 cm longer than the 2-ocean fish, and the males of both size groups are between 2 and 3 cm larger than the females.

Between years there are pronounced differences in the proportion of 2- and 3-ocean fish and, to a much smaller extent, in the sex ratio of the total runs. Since during the middle part of the Nushagak fishery considered here, the mesh size of the gill nets remained stable at 5½ inches, the total fishing mortality generated by one unit of gear changed from year to year primarily with changes in the relative proportion of 2- and 3-ocean fish and males and females. Consequently, the coefficient of catchability must be determined by length or age groups, and separately for males and females. There are only 5 years, 1946-1950, with records of catch and escapement when sailboats were used together with linen gill nets. Conversion to powered fishing boats was largely accomplished by 1954, although a shift in boat types continued. At the same time nylon gill nets came into universal use. Added to these changes were modifications of boundary lines of the fishing districts. Therefore, the rate of the present-day fishing of the gear in Bristol Bay is not comparable with that which prevailed during the middle period of the Nushagak fishery.

Data on catch and escapement and the corresponding length-frequency distributions for Nushagak from 1946-1950 are available (Mathisen et al., 1963). The escapements were estimated visually and may not be too accurate. But in 1 year, 1946, when an independent estimate could be made from a tagging experiment, the correspondence was remarkably great (Mathisen, 1969). Effort during the same years is listed in Table 5. On the assumption that set net effort can be converted into drift net effort and that all units of gear were fishing simultaneously on the same stock, it is a straightforward matter of computing the coefficient of catchability for each centimeter group and separately for males and females from the expression on page 754 used in reverse.

There were rather large year-to-year variations; therefore the following smoothing process has been applied to the data. An arithmetic mean value for each centimeter group was found for the 5 years considered. A moving average of 5's of these arithmetic means provided the final values in the selection curves in Figure 4. The dip in the selection curve for males is con-

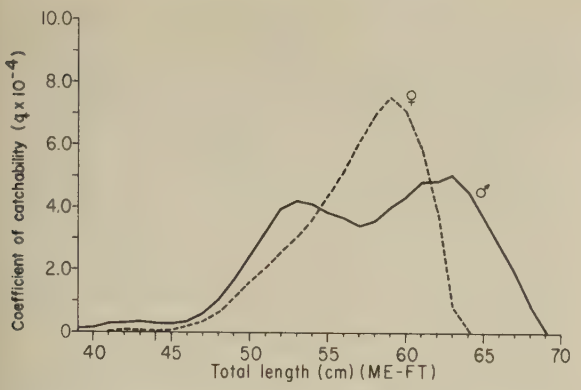

FIGURE 4.—Instantaneous rate of fishing by centimeter groups.

sidered due to statistical variability introduced by the rather small escapements in 1949 and 1950. It was further demonstrated by similar calculations for recent years with exact catch and escapement data that once the males become vulnerable to the gear, the coefficient of catchability increases only slightly from 2- to 3-ocean fish. Whereas in the lower part of the selection range, the curves are fairly similar for males and females, the rate of fishing on 3-ocean females was several times that of 2-ocean females based on the average lengths of these two groups given by Mathisen et al. (1963). As a result, in years when 2-ocean fish predominated in the run, a large preponderance of females was present in the escapement as in 1946, when there were 68% males in the catch and only 35% males in the escapement. In 1948, when there was a predominance of 3-ocean fish, the corresponding figures were 44% and 49%.

The selective action of the gill nets on the 3-ocean fish can be demonstrated further by comparison of age composition of gill net and trap catches made in the same year (Table 6). The traps can be considered nonselective and were placed close to the upper boundary line of the fishing area (Moser, 1902). Therefore, the age composition of the trap catches can be used as an estimate of the age composition of the escapement. Whereas the 2- and 3-ocean fish were present in about the same numbers, the catch by 5¾-inch gill nets contained more than five times as many 3-ocean fish as 2-ocean fish.

TABLE 6.—Age composition in trap and gill net catches in Nushagak, July 1 and 5, 1919.

Age group	Traps		Gill nets	
	Number of fish	Percent	Number of fish	Percent
1.2	65		14	
2.2	33		15	
2-ocean	98	51.9	29	15.5
1.3	83		150	
2.3	8		8	
3-ocean	91	48.1	158	84.5
Total	189		187	

Source: Clark, Frances N. 1933. Red salmon in the Nushagak District of Bristol Bay Alaska. (U.S. Bureau of Fisheries) Natl. Mar. Fish. Serv., Biol. Lab., Auke Bay, Alaska. (Unpublished manuscript.)

ESTIMATED ESCAPEMENTS, 1925-1945

When the calculations outlined above are executed, an estimated escapement for each of the years from 1925 to 1945 is obtained (Table 7). Two years, 1932 and 1938, were not included in the computation of an average escapement level since no length measurements were taken in these years. No measurements were taken in the fishery in 1931; instead, scales and measurements were collected in the Wood River, and this length-frequency distribution has been

TABLE 7.—Calculated escapements and total runs in Nushagak District, 1925-1945.

Year	Total catch	Total escapement	Estimated total run	Escapement as percent of total run
1925	3,903,120	285,081	4,188,201	6.8
1926	4,022,333	697,730	4,720,063	14.8
1927	657,468	803,643	1,461,111	55.0
1928	4,957,072	1,383,130	6,340,202	21.8
1929	3,851,482	754,125	4,605,607	16.4
1930	1,610,568	3,158,751	4,769,319	66.2
1931	2,260,539	491,877	2,752,416	17.9
1932	3,083,165	--	--	--
1933	3,753,230	1,995,688	5,748,918	34.7
1934	4,575,043	1,791,481	6,366,524	28.1
1935	649,093	2,277,858	2,926,951	77.8
1936	1,560,135	1,816,382	3,376,517	53.8
1937	4,561,297	10,118,033	14,679,330	68.9
1938	2,322,704	--	--	--
1939	4,169,122	361,356	4,530,478	8.0
1940	1,519,082	990,237	2,509,319	39.5
1941	1,897,870	1,197,981	3,095,851	38.7
1942	2,465,779	1,586,861	4,052,640	39.2
1943	3,373,650	1,762,232	5,135,882	34.3
1944	3,513,236	1,335,734	4,848,970	27.6
1945	2,296,020	1,614,470	3,910,490	41.3
Total	61,002,458	34,422,650	90,018,789	--
Average 1925-1945	2,904,879	1,811,718	4,737,831	38.2

used. Since the fish in the escapement average smaller than in the catch, it will result in an overestimate of the total run for this year.

Unquestionably, the computed escapements are subject to many sources of error, and they reflect only the general magnitude of the escapements. In general there are some measurements from each fishing period that can be weighted by the corresponding catches, and any unrepresentativeness of the sampling was in part corrected. It therefore appears that the greatest bias arises from the way in which fish were selected and measured. In 1930, for example, there were few measurements taken, and they included a rather high proportion of suspiciously small 2-ocean females, which resulted in the rather large estimated total escapement. Almost 12,000 measurements were made in 1937, but largely of fish from the resident set net fishery near the upper fishing boundary. The result is an underestimate of the mean average length in the commercial catches, since the run at this point had been subjected to the selection of the drift net fishery; the calculated escapement is substantially inflated. In 1939 no 2-ocean fish were measured in drift net catches, and therefore the low rate of escapement may be substantially correct.

The International North Pacific Fisheries Commission (1962) has published estimates of Nushagak escapements for the period considered here. A fishing rate common for all size groups, and with no distinction between males and females, was computed from Bristol Bay catch and escapement data for 1955-1957. Furthermore, nylon gill nets were used and were operated from power boats. Because of the selective action of the gill nets for males and females, and for 2- and 3-ocean fish, it is easy to understand that these estimates are entirely different from those presented here.

SUMMARY OF RESULTS

On the previous pages, escapement levels were calculated for the three distinct periods of the Nushagak fishery shown by the catches on Figure 2. These results have been summarized in Table 8.

TABLE 8.—Rate of exploitation in three periods of the Nushagak fishery.

Period	Average escapement	Average catch	Exploitation
	Thousands	*Thousands*	*%*
1908-1919	1,126	4,796	81
1925-1945	1,812	2,905	62
1946-1966	1,385	1,183	48

During the early period of the fishery, the runs sustained a fishing mortality of more than 80% until 1919 when all runs to Bristol Bay suffered a drastic decline. The universality of this decline in many sockeye salmon systems suggests that the causes must be sought in changes in the environment and not in the mode of fishing operation. The Nushagak runs never returned to their former level, in contrast to those of the other systems in Bristol Bay, notably those to the Kvichak River.

During the middle period, here defined as the time from 1925 to 1945, the amplitude of the year-to-year oscillation increased (Figure 2).

Following the last World War, not only did the Nushagak and other Bristol Bay sockeye salmon runs decline, but many of the Kamchatka salmon runs did too (Krogius and Krokhin, 1956). The widespread decline suggests again that environmental and probably oceanographic conditions not related to fishing depressed the survival. In the third period of the Nushagak fishery the runs remained at a very low level, compared with levels of the two previous periods.

Concomitant with this stepwise decline in average yield, there has been a decrease of the reproductive potential of the Nushagak sockeye salmon runs. Whereas during the early period of the Nushagak fishery, the runs were exposed to an exploitation rate of nearly 80%, during the middle period of the Nushagak fishery, the runs were exposed to an exploitation rate of around 60%. During the last period, the exploitation rate was around 50%, largely set by the regulation. The runs are maintaining themselves, but so far no substantial increase is apparent.

Thus the rate of return per spawner has fallen from five to less than three and finally to two mature fish. As a result, there has been no increase to former run levels in spite of the reduced

exploitation rates. This situation is in contrast to the situation in the Fraser River, where the removal of the Hell's Gate blockade and increased escapements initiated almost an immediate increase in the returns in some river systems.

Therefore, it remains for us to explore if any changes have occurred in the Nushagak runs that can explain the described reduction in reproductive potential.

DISCUSSION

No visible changes have taken place in the Nushagak environment since fishing commenced there before the turn of the century. Even today there are no dams or any other obstruction to the migrating salmon. The resident population still remains so low that pollution problems or any form of industrial waste are nonexistent. Neither has the subsistence fishery increased in volume and an estimated 30,000 or more of all species are harvested today. Other freshwater fishes were not or were lightly harvested until recent years, when a recreational fishery for trout and char has developed.

A sockeye salmon run to a watershed such as the Nushagak District is made up of a great number of races that differ in morphological features, age structure, time and place of spawning, and reproductive rate. The most direct effect of overfishing would be the disappearance of certain races, or at least a reduction in their numerical size to the point where they cease to be important contributors to the commercial catches. If this were true, it could manifest itself on the spawning grounds after the various races have segregated. The number of spawners per unit of nursery area reflects the stock strength on a spatial basis.

There are some river systems within the Nushagak District with low spawning density relative to that of others. For 1955-1962 the average number of spawners per square kilometer of lake rearing area in the Tikchik Lakes was 280 and in Lake Nunavaugaluk 290. In contrast, the spawning density in the Wood River lakes was 2,340 fish per square kilometer of lake rearing area and 4,360 fish in the Igushik system (Burgner et al., 1969). There is no evidence available to indicate that this was different in the early history of the Nushagak fishery. While there are relatively more 3-ocean fish in the Tikchik runs than elsewhere in the Nushagak system and hence a higher fishing mortality, the scarcity of spawning beaches and streams precludes both here and in the Nunavagaluk system the possibility of a large population prior to commercial exploitation.

The possibility still remains that the individual races may pass through the fishery at different times and thereby be exposed to different fishing rates. If this were so, one might expect to see some shift in time when peak abundance occurred. This was studied by plotting the dates when 10, 50, and 90% of the commercial catches were made (Figure 5). From 1895 to 1947, the two first points were reached at the same time aside from simultaneous year-to-year variations. There are some indications in Figure 5 that salmon were present longer in Nushagak Bay in years prior to 1920, but when one considers the exponential rate of departure to the spawning streams from the fishing grounds, the larger total runs during these years would account for such a prolongation of the fishing season. Added to this consideration is the fact that the canneries

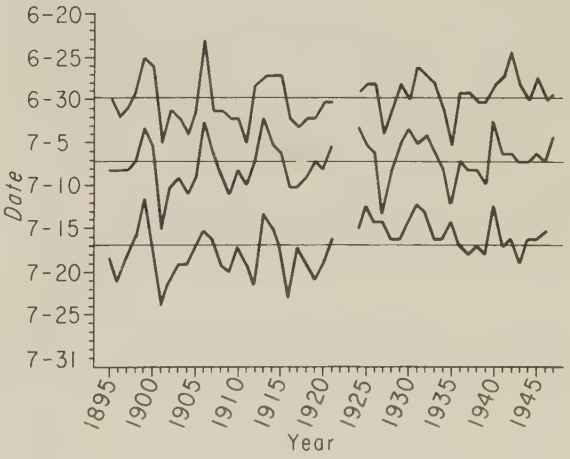

FIGURE 5.—Data on which 10, 50, and 90% of the Nushagak catch was made, 1895-1947. (Subsequent years omitted since a progressively stricter curtailment of fishing time prevented direct comparison with former years.)

usually set production goals in this period and extended fishing until these goals were reached.

As a result, one may conclude that 70 years of intensive harvesting have not drastically affected the timing of the Nushagak runs. All tagging experiments conducted in Bristol Bay point to a complete mixing of all races in the fishery and exposure to the same fishing pressure in a specific river system (Smith, 1964; Mathisen, 1969; Straty, 1969). Thus there is very little evidence of a differential rate of removal in time among all the races that constitute the Nushagak sockeye salmon run. The only exception seems to be the races bound for the Igushik system. Their migration path follows the west side of Nushagak Bay past Nichol's Spit. In earlier years when the main fishing activities were concentrated closer to the confluence of the Nushagak and Wood Rivers than they are today, the fishing pressure on the Igushik races during those years was lower.

A differential fishing pressure could arise from the selectivity of the gill nets if some Nushagak races consisted primarily of 3-ocean fish while in others 2-ocean fish predominated. Burgner (1964) has pointed out the preponderance of 3-ocean fish to the Tikchik as one example. However, if a diminution of such races were of any real consequence, it must manifest itself in changes of the age composition through the recorded history of the Nushagak fishery. The figures in Table 9 are based on the age composition in the commercial catches. Because of the larger net sizes used up to 1926, a bias is introduced in favor of 3-ocean fish and only the last two periods are directly comparable.

Throughout all years the majority of the fish migrated to sea as age 1 smolts and returned in somewhat the same proportion of 2- and 3-ocean fish. Over the years one can notice a shift, with less 3-ocean fish in the catches of males in recent years. If similar data were available for the escapement, and thereby of the total runs, one would in all probability see more of a contrast in the shift from 3- to 2-ocean female fish, especially in the years when mesh sizes were larger than 5½ inches. A mesh size experiment conducted in 1928 by the Bureau of Fisheries illustrates this point. The log ratio of catches made with nets of 5½-inch and 6-inch mesh sizes are plotted by centimeter groups in Figure 6 and form an expected straight line. The aberrant points toward the upper size range are due to a much larger sampling error because of the very few fish present at these sizes.

The essential element of an escapement is not the total number of fish present but the potential egg deposition they represent. During the first period of the Nushagak fishery, when net sizes ranged from 6¼ to 5¾ inches, escapements of the same numerical magnitude as in later years must have represented a substantially higher potential egg deposition since a much higher proportion of 3-ocean females was included in those escapements than in years with 5½-inch mesh size. On the average, 3-ocean females produce 650 eggs more per female than 2-ocean fish. The mean fecundity of these two groups are 3,639 and 4,290 eggs, respectively (Mathisen, 1962).

This net selection has another, more intangible aspect. Not only is fecundity greater in the larger 3-ocean females, but egg size is also a function of the size of the females (Mathisen, 1962). Thus there may be a higher survival of the progeny in this case than from eggs produced by 2-ocean females in the same environment. This concern was expressed in 1927 by

TABLE 9.—Summary of age in the commercial catches of sockeye salmon in Nushagak.

Sex	Period	Age-groups					No. of years sampled	2-ocean	3-ocean
		1.2	2.2	1.3	2.3	Others			
Male	1912-1919	21.32	8.66	57.08	11.11	1.83	6	21.98	68.19
	1925-1945	35.77	8.95	48.16	5.38	1.59	18	44.82	53.54
	1946-1966	42.19	9.55	40.77	4.12	3.37	21	51.74	44.89
Female	1912-1919	27.11	9.80	51.25	11.08	0.76	6	36.91	62.33
	1925-1945	25.42	7.05	60.48	4.97	1.43	18	32.47	65.45
	1946-1966	27.12	5.91	56.62	5.57	4.78	21	33.03	62.19

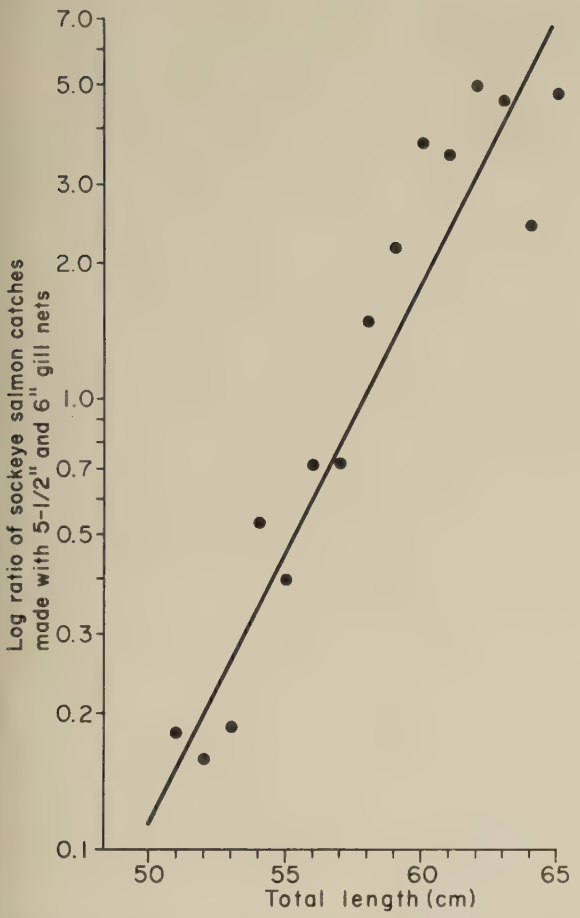

FIGURE 6.—Log ratio of catches made in Nushagak, 1928, by 6- and 5½-inch gill nets. Males and females combined by centimeter groups.

Gilbert, who wrote in a letter to Commissioner H. O'Malley:

> As a result of this screening process, we are selecting for breeding purposes predominantly the younger or less robust members of the colony, those that are dwarfed by reason of early maturity or lack of growth vigor. The effect of such continued breeding from the least fit of the community must result, it would seem, in the gradual impoverishment of the race and the reduction in size and value of the individuals composing it.

The inference may be made that the observed shifts in run strength and productivity in Nushagak are associated with changes in gear selectivity, by a shift to smaller net sizes over the years which reduced the potential egg deposition rather than the numerical size of the escapements. Such an explanation would be most appropriate for the transfer from the first to the second major period of the Nushagak fishery in 1919. But this argument loses some strength when other sockeye salmon systems outside Bristol Bay are considered.

The given description of the Nushagak fishery and reduction of reproductive rate are almost identical to that described for the Karluk sockeye fishery by Rounsefell (1958). A major portion of the Karluk River catches were taken in beach seines at the river mouth or in adjacent traps, both of which are nonselective for size. Gill nets never played a dominant part in harvest of the Karluk sockeye salmon. In spite of the absence of gear selective for size, a selection from the middle part of the run was present (Thompson, 1951).

The Chignik fishery offers another example. Recently Dahlberg (1968) and others before him have pointed out the almost identical catch curves for the Chignik and Nushagak fishery. In the Chignik fishery one can distinguish three major production levels, and the relative position of these are the same as observed in Nushagak (Figure 7). The only difference is that the fall from an initial high production level to an intermediate one came a few years later, 1926-1927, in the case of the Chignik fishery. Traps were for a long time the principal fishing

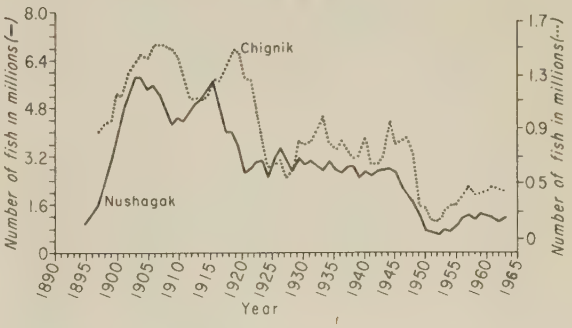

FIGURE 7.—Comparison of catches of sockeye salmon in the Chignik and Nushagak fisheries. Curves smoothed by a moving average of 5's.

gear at Chignik, later supplemented with seines, which today are the only gear operated. Gillnetting never became effective at Chignik because of the clear water there and the narrow channel. But as in the case of the Karluk fishery, there has been a selection and domination of certain races (Dahlberg, 1968).

In three important sockeye-producing systems, the historical development has been the same and resulted in a continuous decline of return per spawner. Dahlberg sees the cause as differential fishing mortality on the Chignik Lake and Black Lake races with an overfishing on the latter ones. Rounsefell (1958) suspects the effect of predation and stabilization of predator populations in the absence of the former large contrast between off and peak years as the principal cause. The evidence presented for the Nushagak fishery points to various effects of net selectivity as a major contributing factor. Viewed by themselves, each of the presented explanations may appear plausible, but the almost identical happenings in three unrelated systems suggest that a common underlying cause also may be operating.

In all three cases the decline started two decades or so after large-scale commercial harvest had been in operation. Provided the initial rate of reproduction remained the same the spawning stock or the potential egg deposition was sufficient to maintain the runs, or rebuild them after stringent regulations were put into effect.

One might conclude that the primary production of the nursery areas, which all are oligotrophic lakes in the three mentioned systems, started a slow decline from the moment fishing began, and the enrichment from salmon carcasses was substantially reduced relative to the situation which prevailed prior to commercial harvest.

Clearly, a hypothesis of this type cannot be demonstrated from the data presented. Rather, conclusive evidence must be sought from other sources. One is descriptive and involves a study of the sedimentation rates in prefishing years and in recent ones from bottom cores. Great changes in basic lake productivity should be reflected in the yearly sedimentation rate of diatom shells. Donaldson (1967) has demonstrated that changes in escapement level are indicated by phosphorus content of corresponding bottom sediments.

Experimental evidence on the role of the biogenic enrichment from salmon carcasses can be obtained from a lake fertilization similar in content, volume, and mode of dispersion to that provided by the dying spawners themselves.

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CHANGES IN CATCH AND EFFORT IN THE ATLANTIC MENHADEN PURSE-SEINE FISHERY 1940-68

WILLIAM R. NICHOLSON[1]

ABSTRACT

The catch, number of vessel weeks, and catch per vessel week in the Atlantic menhaden fishery increased during the 1950's. During this period fishing methods improved and the efficiency of vessels increased. Improvements included use of airplanes for spotting schools, aluminum purse boats, nylon nets, power blocks, and fish pumps for catching and handling fish, and larger and faster carrier vessels that could range farther from port. The catch and catch per vessel week began declining north of Chesapeake Bay in the early 1960's. By 1966, fish north of Chesapeake Bay had become so scarce that plants either closed or operated far below their capacity. In Chesapeake Bay the number of vessel weeks increased, and the catch and catch per vessel week decreased through the early and mid 1960's. Variations in catch, effort, and catch per unit of effort showed no trends in the South Atlantic. The annual mean number of purse-seine sets per day varied in different areas and ranged from about 2.0 to 4.5. The annual mean catch per set ranged from about 11 to 25 metric tons.

Catch and effort statistics are important in evaluating and managing any fishery. They may be used in measuring changes in actual or apparent abundance, estimating population sizes and mortality rates, and determining optimum fishing rates.

When investigations of the Atlantic menhaden (*Brevoortia tyrannus*) fishery were begun in 1955 by the Bureau of Commercial Fisheries, provisions were made for collecting and compiling catch and effort statistics. The number and locations of daily purse-seine sets were obtained from logbooks placed aboard vessels at the beginning of the fishing season, and daily catches of individual vessels were copied from plant records.

The objectives of the present study were: (1) to analyze logbook data and vessel landing records to determine differences and changes in the number of purse-seine sets, mean number of sets per day, and the mean catch per set, both between and within geographical divisions of the fishery, (2) to develop a method of measuring fishing effort, and (3) to document changes that have occurred in the fishery.

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BRIEF HISTORY OF THE FISHERY

Atlantic menhaden are found from central Florida to Nova Scotia and at one time or another have been exploited over most of this range. Fishing began in the early part of the 19th century in waters off Massachusetts and Maine. Following improved methods of fishing, extracting oil, and processing meal, the fishery expanded in this area in the latter part of the 19th century. When the scarcity of menhaden in waters north of Cape Cod caused the collapse of the fishery in that area, about 1895, the industry shifted to the Middle and South Atlantic coast. By the 1930's processing plants were located in approximately the same areas where they occur today (Figure 1).

Although in some areas pound nets capture menhaden incidentally with other species, purse seines catch nearly all of the fish that are reduced for meal and oil.

Purse seining began in the late 19th century and by present standards was inefficient and laborious. Purse boats were rowed and carrier vessels were sailed. Gradually, sailing vessels were replaced by larger, coal burning steam ships, purse boats were equipped with gasoline

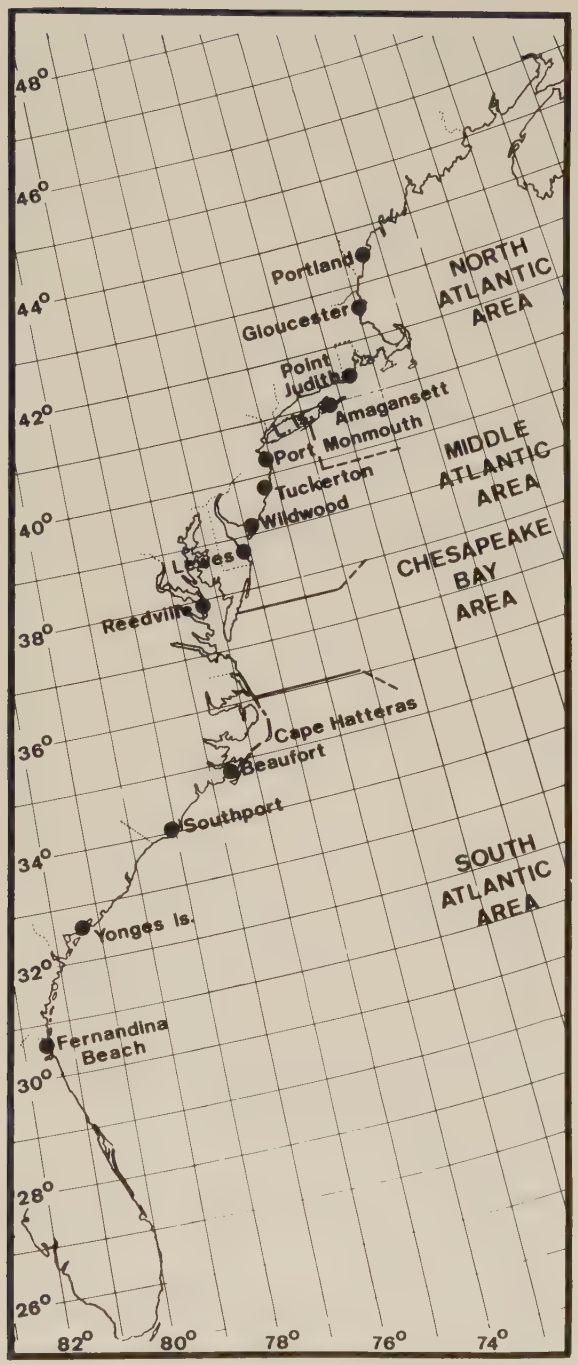

FIGURE 1.—Ports and major fishing areas, Atlantic menhaden fishery.

engines, and seines were made larger. Following World War I, diesel and gasoline engines gradually replaced steam engines in the carrier vessels. Methods of catching and processing menhaden, however, changed very little between World Wars I and II.

After World War II the increased demand for fish meal and oil initiated changes in the industry. Numbers and sizes of vessels increased, methods of fishing changed, processing facilities expanded, and processing efficiency increased.

A major change in fishing methods occurred in 1946 when airplanes were introduced to locate concentrations of fish. Plant operators found this practice so successful that they rapidly added more planes in following years (Table 1). Initially, airplanes scouted wide areas and directed vessels to places where menhaden were abundant. Later, after captains were given portable radios, the airplane pilot directed the actual setting of the net. Since about 1950 airplanes have been an integral part of fishing operations (Robas, 1959; June, 1963).

Fish pumps, initially installed on carrier vessels in 1946, were the first significant advance

TABLE 1.—Number of airplanes used in the Atlantic menhaden fishery.[a]

Year	North Atlantic	Middle Atlantic	Chesapeake Bay	South Atlantic	Total
1945	0	0	0	0	0
1946	0	1	1	0	2
1947	0	7	1	2	10
1948	1	8	1	2	12
1949	1	11	1	2	15
1950	1	10	1	3	15
1951	1	10	1	3	15
1952	2	11	1	4	18
1953	4	11	1	4	20
1954	4	12	3	4	23
1955	5	15	5	4	29
1956	6	15	8	4	33
1957	8	15	9	4	36
1958	8	17	10	4	39
1959	7	17	12	5	41
1960	5	16	7	4	32
1961	6	16	8	4	34
1962	6	16	9	3	34
1963	5	16	11	3	35
1964	4	18	13	4	39
1965	3	6	18	4	31
1966	1	4	18	4	27
1967	0	2	16	4	22
1968	1	2	16	4	23

[a] Exact data are not available for the North Carolina fall fishery. Estimates indicate that 20 to 25 were used each year after about 1955.

in fishing methods after World War II (Robas, 1959). Pumping fish directly from the purse seine to the hold replaced the time-consuming method of brailing and left more time for scouting and making additional sets. By 1955 nearly all vessels were equipped with fish pumps (Table 2).

Before fish in the seine can be pumped or brailed aboard the carrier vessel, they must be concentrated, or "hardened-up." This can be done by crewmen in the purse boats pulling in the net by hand, but it is a laborious process that requires approximately 22 men. A mechanical device, or "power block," for "drying-up" the net, used experimentally in 1955, became operational in 1956 (Schmidt, 1959a). Its use reduced the crew by 6 to 10 men and the average time to "harden-up" the fish by about 6 min (Schmidt, 1959a, 1959b), and enabled the crew to retrieve the net quickly if the fish were missed. Power-blocks were used extensively for the first time in 1958 and by 1966 were installed on nearly all vessels from Long Island southward (Table 2).

Large sets are sometimes lost when the net cannot be raised manually or mechanically to concentrate the fish so that they may be pumped. But the pump head, if positively charged with electricity, becomes an electrode that attracts and concentrates menhaden without the necessity of raising the bunt (Kreutzer 1959). Such a device, commonly called a "fish shocker," was first installed on vessels in 1956, but its use did not spread beyond the Middle and North Atlantic areas. By 1966 it had fallen into disuse (Table 3).

Beginning in 1954, nylon nets gradually replaced cotton or linen nets (Table 3). Although more expensive initially, nylon nets last longer and do not split or tear when filled with fish as other nets sometimes do.

Aluminum purse boats began replacing wooden purse boats in 1957 (Table 3). Being lighter, more maneuverable, and more stable than wooden boats, they can encircle a school of fish easier

TABLE 2.—Percent of vessels equipped with fish pumps and power blocks in the Atlantic menhaden purse-seine fishery.

Year	Middle Atlantic[a]		Chesapeake Bay		South Atlantic	
	Fish pumps	Power blocks	Fish pumps	Power blocks	Fish pumps	Power blocks
1946-49	0	0	10-20	0	0	0
1950	6	0	24	0	0	0
1951	13	0	25	0	0	0
1952	32	0	31	0	0	0
1953	44	0	22	0	9	0
1954	48	0	25	0	10	0
1955	81	0	90	0	11	0
1956	78	2	92	0	23	0
1957	91	2	88	16	23	0
1958	96	100	100	57	25	0
1959	100	100	100	68	45	0
1960	100	100	100	95	45	0
1961	100	100	100	74	45	0
1962	100	100	100	66	50	31
1963	100	100	100	83	69	31
1964-68	100	100	100	100	64-74	42-69

a Includes Amagansett from North Atlantic Area.

TABLE 3.—Percent of vessels equipped with fish shockers, nylon nets, and aluminum purse boats in the Atlantic menhaden purse-seine fishery.

Year	Middle Atlantic[a]			Chesapeake Bay			South Atlantic		
	Fish shockers	Nylon nets	Aluminum purse boats	Fish shockers	Nylon nets	Aluminum purse boats	Fish shockers	Nylon nets	Aluminum purse boats
1954	0	2	0	0	0	0	0	0	0
1955	0	5	0	0	0	0	0	0	0
1956	47	19	0	0	4	0	0	0	0
1957	45	18	0	0	44	0	0	13	0
1958	85	100	66	0	82	4	0	14	0
1959	85	100	85	0	94	23	0	20	0
1960	82	100	82	0	100	32	0	45	0
1961	82	100	82	0	100	30	0	58	0
1962	82	100	89	0	100	63	0	81	33
1963	82	100	100	0	100	83	0	100	50
1964	78	100	100	0	100	100	0	100	50
1965	86	100	100	0	100	100	0	100	58
1966	0	100	100	0	100	100	0	100	69
1967	0	100	100	0	100	100	0	100	100
1968	0	100	100	0	100	100	0	100	100

a Includes Amagansett from North Atlantic Area.

and faster, and can operate more easily in rough seas.

Three jet-propelled purse boats were introduced in 1962. Adjustable jet nozzles on each end gave the boats excellent maneuverability, and there was no propeller or guard to entangle nets. They lacked the power to close up the seine rapidly, however, and were abandoned.

With the exception of airplanes for spotting, none of the improvements were adopted by vessels in the Point Judith, Gloucester, or Portland fleets. All vessels fishing from these ports were small to medium-sized otter trawlers that were converted to purse seining for only about 2 months during the summer.

DESCRIPTION OF THE FISHERY

The purse-seine season for menhaden extends from late spring through fall, but the time varies in different localities. South of Cape Hatteras, N.C., it begins in April or May and lasts until late December or early January. From Chesapeake Bay to the southern shore of Long Island it begins in late May and usually ends about the third week in October. North of Cape Cod the season lasts only from about late June to early September.

To facilitate summarizing and discussing annual changes in the fishery, June and Reintjes (1959) divided the range of Atlantic menhaden into four areas, the North Atlantic, Middle Atlantic, Chesapeake Bay, and South Atlantic (Figure 1). Although the boundaries are arbitrary, they were drawn to take advantage of natural separations in the fishing areas. Similarities in age and size composition of the catches, time and duration of fishing, and range of vessels from the home port tended to set each area apart. The North Carolina fall fishery, a specialized fishery that occurs only during November and December from Cape Hatteras to Cape Fear, is distinct from the summer fishery in the South Atlantic and was treated as if it were an area. This classification, which provides a convenient way of expressing statistics of the fishery, is used in the present analysis. Ports in the South Atlantic area are Fernandina Beach, Fla.; Yonges Island, S.C.; and Southport and Beaufort, N.C.; in the Chesapeake Bay area—Reedville, Va.; in the Middle Atlantic area, Lewes, Del.; and Wildwood, Tuckerton, and Port Monmouth, N.J.; in the North Atlantic area—Amagansett, N.Y.; Point Judith, R.I.; Gloucester, Mass.; and Portland, Maine; and in the North Carolina fall fishery—Beaufort and Morehead City, N.C.

A disadvantage of the fishery area concept is that all of the fish landed at a port in a particular area may not have been caught in that area. The problem is not serious, however, because vessels seldom fish in areas other than the one in which their home port is located. Port Monmouth vessels, which sometimes go through the East River to fish in western Long Island Sound, and Amagansett vessels, which sometimes fish off the northern New Jersey coast, contradict this general rule more often than do vessels at other ports.

The number and location of daily purse-seine sets each year from 1955 to 1966 were obtained from logbooks placed aboard vessels at the beginning of each fishing season. Port samplers were instructed to pick up copies of each page every 2 weeks, answer questions pertaining to the methods of keeping the logs, and stimulate interest of the pilots to keep the logs complete and up to date. From 25 to 100% of the boats fishing at each port kept logs. Although generally over 60% of the fleet was covered each year, many vessels did not keep complete records.

Daily landings of each vessel were copied from plant records. Although some records extended back as far as 1912, records at most plants were not available for years prior to 1940.

ANNUAL CATCH

No trends were evident in the annual catches in the South Atlantic area or North Carolina fall fishery, but the catches in the other three areas reflected an increase in fishing effort after 1945 and a decline in abundance after 1956 (Table 4). After reaching a peak in 1956 of 378,300 metric tons in the Middle Atlantic area and 98,500 tons in the North Atlantic area, the catch declined to 6,000 and 1,800 tons, respectively in 1966. In the Chesapeake Bay area the catch decreased from 196,800 metric tons in

1959 to 115,600 tons in 1966. In the North Atlantic area, the Point Judith, Gloucester, and Portland fleets, which began menhaden fishing about 1949, accounted for most of the increases between 1950 and 1960. Menhaden were not landed at Portland after 1957 or at Gloucester and Point Judith after 1962.

CALCULATION OF FISHING EFFORT

In any searching fishery where the sizes and types of vessels vary, the unit of fishing effort is difficult to define. Marr (1950) found a positive linear relation between mean catch per boat week and boat length in the Pacific sardine (*Sardinops sagax*) fishery off Oregon. He selected the modal boat-length group as a standard, calculated the catch per boat week of boats in this group for each year, and based his estimates of apparent abundance on this index. He was unable, however, to estimate total effort except by dividing the total catch of all vessels by the catch per unit of the standard group.

Silliman and Clark (1945), studying the Pacific sardine fishery off California, linked groups of identical vessels and estimated apparent abundance from the catch per boat week of these groups. They estimated the total effort by dividing the total catch by the catch per boat week of the linked group, assuming that the catch per boat week of the selected vessels was representative of the catch per boat week of the fleet, and using a base season for each of the three areas they studied. Recognizing the effect of differences in vessel size on catch per unit of effort, they used a standard multiple regression to estimate total effort in each area by relating in a single equation the length and horsepower of each vessel, the number of vessels, and the number of weeks.

Clark and Daugherty (1950) extended the study by Silliman and Clark through the 1948-49

TABLE 4.—Atlantic menhaden purse-seine catch by year and area.

Year	Area					Total
	North Atlantic	Middle Atlantic	Chesapeake Bay	South Atlantic	North Carolina fall fishery	
	thousands of metric tons					
1940	16.8	91.1	35.3	37.9	36.6	217.7
1941	33.5	104.1	60.2	45.2	34.9	277.9
1942	14.6	77.7	21.9	32.9	20.1	167.2
1943	9.8	96.8	42.1	59.7	28.8	237.2
1944	27.5	122.6	32.2	46.9	28.7	257.9
1945	34.0	136.4	35.1	58.5	31.9	295.9
1946	42.9	183.8	57.6	40.8	37.3	362.4
1947	44.2	185.8	81.2	34.2	32.9	378.3
1948	44.4	137.4	68.3	55.8	40.6	346.5
1949	52.2	149.8	62.8	59.3	39.7	363.8
1950	49.3	143.0	63.1	20.0	21.8	297.2
1951	51.0	168.6	56.1	54.6	31.1	361.4
1952	58.1	193.7	45.7	86.0	26.4	409.9
1953	59.7	363.2	77.8	52.8	39.7	593.2
1954	64.9	335.7	126.0	39.6	41.9	608.1
1955	83.3	317.6	132.7	43.4	64.4	641.4
1956	98.5	378.3	94.0	68.6	72.7	712.1
1957	83.5	304.5	126.4	36.4	52.0	602.8
1958	36.0	211.1	151.3	41.3	70.3	510.0
1959	66.0	250.9	196.8	63.1	82.3	659.1
1960	66.4	256.0	108.5	36.7	62.2	529.8
1961	58.6	274.6	128.7	44.1	69.9	575.9
1962	64.7	249.9	155.1	42.2	25.8	537.7
1963	35.2	111.7	104.0	34.2	62.8	347.9
1964	15.0	35.2	134.1	46.5	38.4	269.2
1965	11.9	45.8	126.1	36.7	52.9	273.4
1966	1.8	6.0	115.6	24.5	71.7	219.6
1967	0	17.1	91.1	34.1	51.2	193.5
1968	6.7	26.2	115.5	33.6	52.8	234.8

season. They also used linked groups of vessels, but simplified calculations by using catch per lunar month rather than catch per week.

June and Reintjes (1957), studying the menhaden fishery off Delaware Bay, used the linkage method to determine the catch per boat week for selected boats from 1939 to 1953. They estimated the total number of boat weeks by dividing the total catch by the catch per boat week.

In the yellowfin tuna (*Thunnus albacares*) bait-boat fishery in the eastern tropical Pacific, Shimada and Schaefer (1956) grouped vessels by carrying capacity. They computed the catch per days absence from port for each group and established one group as a standard. They standardized effort by dividing the catch per days absence of the standard group by the catch per days absence of each other group. Broadhead (1962) related the catch per day of bait boats to the catch per day of purse-seine vessels by using regression analysis.

Menhaden plant records, while showing the date and amount of fish landed by each vessel, do not list days when vessels fish and catch nothing, and do not indicate whether a catch represents 1 or more days' fishing. While vessels generally land their catch daily, quite often in the Middle and North Atlantic areas they land 2 or 3 days' catch at one time, particularly in late spring and early fall, a practice which has increased in recent years as fish have become scarce and daily catches smaller.

There is no satisfactory way of getting the complete daily history of each vessel. Even if port samplers recorded each vessel's daily activity, the records still would be incomplete because not all ports are sampled and because no ports were sampled prior to 1955. Logbook records also are incomplete. Any effective method of measuring effort, therefore, must use vessel landings as they are recorded at the plants.

Fortunately, menhaden vessels generally operate continuously throughout all or part of the fishing season and fish every day that weather permits, unless in port for repairs. Except in the North Carolina fall fishery, which lasts only 6 to 8 weeks, the number of days that bad weather prohibits menhaden fishing is relatively small and is relatively constant from year to year. Any time period, therefore, that assumes continuous fishing and accounts for unproductive fishing days should be a satisfactory unit of basic fishing effort. Because the vessel week satisfies these conditions and may be readily computed, it was selected as the basic unit.

Because variations in the catch per unit of effort among vessels may necessitate adjusting the basic unit to a common standard, the relative efficiency of vessels fishing from each port was examined.

No clear correlation could be shown between catch per week and vessel length or weight, so the relation between mean catch per week and vessel carrying capacity was explored. Carrying capacity, determined for each vessel by averaging the 10 largest catches for 3 consecutive years, ranged from about 100 to 350 short tons (90-317 metric tons). Vessels were grouped, according to their carrying capacity in short tons, into six classes:

Class	Carrying capacity
1	<141
2	141-180
3	181-220
4	221-260
5	261-300
6	>300

The relative efficiency of vessels at each port was examined by plotting the mean catch per week of each vessel and by plotting the catch per week against carrying capacity.

In the South Atlantic area all vessels were class 3 at Fernandina Beach, Yonges Island, and Southport, and class 1 or 3 at Beaufort. Variation in the catch per week among vessels was evident at all ports, but there was no distinct tendency for any group to have larger or smaller catches per week than another.

Until about 1963 nearly all vessels in Chesapeake Bay were class 3, although a few were class 2, 4, or 5. After 1961 the number of class 5 vessels increased. Although the large capacity vessel tended to have greater mean catches per week than small capacity vessels, the variation was extreme among all vessels, both between and within years. As the catch per week declined after 1961, the variation between vessels of small and large capacities decreased.

In the Middle Atlantic area vessels ranged from class 2 to 6, but no more than two classes occurred at any port. At Port Monmouth and Tuckerton, class 6 vessels did not show substantially greater catches per week than class 5 vessels. Class 5 vessels at Lewes clearly had greater catches per week than class 3 vessels, while class 5 vessels at Wildwood had greater catches per week than class 2 vessels.

Because the increases in the catch per vessel week that accompanied the increases in vessel carrying capacity were small and inconsistent and the variability between ports was great, no vessel class was designated as a standard for the fishery. Effort was simply left unadjusted at all except five ports—Lewes, Wildwood, Point Judith, Gloucester, and Portland.

Effort at Lewes and Wildwood was adjusted because the differences in the catch per unit of effort between the two classes at each port were large. At these ports the 10-year mean of the ratio of the catch per week of the group of larger vessels to that of the group of smaller vessels was computed for 1950-59. Annual effort of the smaller vessels was adjusted by multiplying the total number of weeks fished each year by the mean ratio, 0.610 for Wildwood and 0.573 for Lewes.

Effort at the other three ports was adjusted because many of the vessels, which were small to medium-size otter trawlers temporarily converted to purse seiners during the summer, fished intermittently, usually only when menhaden were plentiful. Because effort could not be measured very precisely under these conditions, it was estimated in terms of Amagansett units by dividing the annual catches at these ports by the mean catch per week of Amagansett vessels.

Most menhaden vessels were class 3, 4, or 5. At most ports the relative proportions of one class to another changed very little each year and the number of vessels remained fairly constant (Table 5). Under such conditions the number of vessel weeks, with minor adjustments, was as precise an estimate of total fishing effort as was possible to obtain. Various other adjustments might have been made, but with doubtful improvement in the overall estimate of fishing effort.

Henceforth, vessel weeks will refer to units of fishing effort and will include these adjustments.

NUMBER OF VESSEL WEEKS

After World War II ended in 1945, the number of vessel weeks rose sharply in the Chesapeake Bay, Middle Atlantic, and North Atlantic areas (Table 6). The increase resulted from the addition of vessels in all areas and from an increase in the number of weeks that plants in the North and Middle Atlantic operated.

After 1959 in the North Atlantic and 1962 in the Middle Atlantic, the number of vessel weeks dropped sharply. Much of the decrease in the North Atlantic between 1959 and 1962 can be attributed to a reduced number of converted trawlers at Portland, Gloucester, and Point Judith, where no menhaden were landed after 1962. After 1962 the number of vessels at Amagansett also declined. Reduced effort in the Middle Atlantic after 1962 was due to a decrease in the number of vessels. The Tuckerton plant and one of the Lewes plants closed during the 1964 season and never reopened. The Wildwood plant operated only a few weeks each year after 1964, and the boats were transferred to plants in Chesapeake Bay. The remaining plant at Lewes closed after the 1965 season.

Effort in the Chesapeake Bay area fluctuated between approximately 300 and 400 vessel weeks from 1944 to 1954; thereafter it generally increased (except when fishing was restricted in 1960 because of a poor market) until about 800 vessel weeks were reached in 1964-66. Additional vessels accounted for most of the increase through 1963. In 1964-68, fishing terminated approximately 7 weeks later (mid-November) than in previous years.

In the South Atlantic area, effort fluctuated between 245 and 530 vessel weeks from 1941 to 1968. Although some fluctuation was due to variation in the length of the fishing season, particularly in Florida, most was due to variations in the number of vessels. The annual number of vessels, and vessel weeks, generally was less from 1960 to 1968 than in previous years.

In the North Carolina fall fishery, the number of vessel weeks varied from 97 to 457 and

TABLE 5.—Number of menhaden vessels fishing at Atlantic coast ports, by class capacity.

Year	Amagansett, N.Y.		Port Monmouth, N.J.		Tuckerton, N.J.		Lewes, Del.		Wildwood, N.J.		Reedville, Va.				Beaufort, N.C.			Southport, N.C.		Fernandina Beach, Fla. and Yonges Is., S.C.
	Class		Class		Class		Class		Class		Class				Class			Class		Class
	5	6	5	6	5	6	3	5	2	5	2	3	4	5	1	2	3	2	3	3
1940	a	a	a	a	0	0	15	4	3	0	2	7	1	0	10	4	0	4	0	a
1941	9	0	a	a	0	0	12	3	5	0	2	12	1	0	6	1	0	5	0	15
1942	9	0	a	a	0	0	16	3	3	0	2	12	1	0	6	1	0	3	0	10
1943	5	0	a	a	0	0	12	1	3	0	1	8	0	0	5	0	0	2	0	15
1944	6	0	a	a	0	0	20	4	3	0	1	9	1	0	6	0	0	3	0	13
1945	6	0	a	a	4	0	10	5	2	0	1	10	1	0	5	0	0	3	0	12
1946	7	0	a	a	5	0	12	7	2	0	1	8	1	0	6	0	0	3	0	8
1947	8	0	a	a	5	0	14	6	2	0	1	13	1	0	5	0	1	3	0	8
1948	9	0	a	a	5	0	20	11	3	0	2	14	1	0	9	2	2	3	0	12
1949	7	2	a	a	6	0	15	10	3	0	1	13	1	0	7	1	2	3	3	14
1950	7	2	a	a	6	0	12	11	3	1	1	13	1	2	5	2	3	3	3	8
1951	8	2	a	a	6	0	12	13	2	2	1	13	1	1	5	2	1	2	3	9
1952	7	2	a	a	6	0	7	11	2	2	1	10	1	1	6	1	2	3	5	10
1953	7	2	a	a	5	1	10	14	3	3	1	16	1	0	6	1	2	3	5	12
1954	7	2	a	a	5	1	10	12	4	3	2	17	1	0	6	1	2	2	5	11
1955	8	2	8	2	5	1	9	16	3	4	2	16	1	1	6	11	2	1	6	14
1956	9	2	7	3	4	2	6	18	2	5	3	19	1	1	6	1	3	1	7	12
1957	8	2	6	4	4	2	6	16	3	5	4	18	1	2	6	1	3	0	7	14
1958	8	2	6	4	4	2	5	15	2	6	4	19	1	4	6	1	3	0	7	9
1959	8	2	6	4	4	2	4	17	2	6	5	21	1	4	7	0	3	0	8	7
1960	8	2	6	4	4	2	4	17	2	8	2	16	1	3	6	0	3	0	8	3
1961	8	2	6	4	4	2	4	17	2	8	3	17	1	2	6	0	3	0	8	3
1962	8	2	6	4	4	2	4	17	2	8	3	17	1	8	5	0	3	0	4	3
1963	8	2	6	4	4	2	3	18	2	7	3	18	1	14	5	0	3	0	5	3
1964	7	2	3	4	4	2	0	15	2	7	2	16	1	19	5	0	3	0	5	3
1965	4	2	1	5	0	0	0	7	0	b	2	13	1	22	5	0	3	0	5	6
1966	3	2	1	4	0	0	0	5	0	b	2	8	1	25	5	0	3	0	3	5
1967	0	0	1	3	0	0	0	0	0	b	0	8	1	23	6	0	2	0	3	5
1968	0	2	1	3	0	0	0	0	0	b	0	6	1	18	6	0	2	0	3	5

a Records not available.
b Variable.

TABLE 6.—Number of vessel weeks per season in the Atlantic menhaden fishery, by year and area.

Year	Area					Total
	North Atlantic	Middle Atlantic	Chesapeake Bay	South Atlantic	North Carolina fall fishery	
1940	a	337	329	a	a	a
1941	141	392	417	506	227	1,683
1942	89	323	251	376	194	1,233
1943	49	287	202	419	166	1,123
1944	84	397	296	316	224	1,317
1945	89	477	302	394	234	1,496
1946	132	528	294	343	291	1,588
1947	134	552	418	322	333	1,759
1948	130	675	405	430	288	1,928
1949	156	691	385	473	457	2,162
1950	155	614	403	322	187	1,681
1951	157	676	369	379	222	1,803
1952	150	580	333	474	220	1,747
1953	161	819	376	474	244	2,074
1954	189	838	408	488	262	2,185
1955	334	890	451	475	342	2,492
1956	298	888	466	530	391	2,573
1957	262	949	527	412	311	2,461
1958	227	734	559	354	380	2,254
1959	301	897	668	474	312	2,652
1960	280	854	410	292	163	1,999
1961	249	946	482	395	224	2,296
1962	264	990	582	327	97	2,260
1963	238	823	666	264	286	2,277
1964	134	376	803	277	249	1,839
1965	96	300	786	359	259	1,800
1966	79	87	795	254	220	1,435
1967	0	124	757	253	212	1,346
1968	23	113	601	245	246	1,228

a Records not available.

depended primarily on the number of vessels, the season generally lasting about 7 or 8 weeks.

CATCH PER VESSEL WEEK

Despite sharp fluctuations that occurred annually, there were pronounced trends in the catch per vessel week in three areas (Table 7). In the North Atlantic area, the catch per vessel week remained at a high level through 1957, dropped sharply in 1958 and continued to decline thereafter. From a peak of 385 metric tons per week in 1952, it dropped to 23 in 1966. The high figure for 1968 (292) reflects the fact that two vessels, one fishing from late June until mid-October and another during August and early September, caught most of the fish available.

The most significant changes occurred in the Middle Atlantic and Chesapeake Bay areas. From 348 metric tons per week in 1946, the catch per vessel week in the Middle Atlantic area dropped to 203 in 1948, and thereafter rose steadily, attaining 444 tons in 1953. From 1954 to 1957 it remained high, between 320 and 426 tons. Between 1958 and 1961, it declined relative to the previous 4 years, but still remained between 279 and 299 tons. It dropped to 253 tons in 1962, and 70 tons in 1966. By contrast, the catch per vessel week in the Chesapeake Bay area was low from 1943 to 1953, fluctuating between 109 and 207 tons, and high from 1954 to 1962, fluctuating, except for 1956, between 239 and 309 tons. In 1963 the catch per week dropped to 156 tons and then continued a downward trend.

In the South Atlantic the catch per vessel week showed no trends. The figures generally ranged from about 86 to 136 metric tons, with extreme fluctuations of from 39 to 180 tons.

In the North Carolina fall fishery the catch per vessel week from 1941 to 1954 fluctuated

TABLE 7.—Mean catch of Atlantic menhaden per vessel week, in metric tons, Atlantic menhaden fishery.

Year	Area				
	North Atlantic	Middle Atlantic	Chesapeake Bay	South Atlantic	North Carolina fall fishery
1940	a	273	107	a	a
1941	237	266	144	89	154
1942	164	240	88	88	104
1943	200	337	208	142	173
1944	327	309	109	149	128
1945	383	286	116	148	136
1946	325	348	196	119	128
1947	329	336	194	106	98
1948	342	203	169	130	141
1949	335	217	163	125	87
1950	318	233	157	62	117
1951	325	249	137	144	140
1952	387	333	136	181	120
1953	371	444	207	111	162
1954	343	401	309	81	160
1955	249	357	294	91	188
1956	330	426	201	130	186
1957	319	320	239	88	167
1958	159	288	270	117	185
1959	219	279	295	133	263
1960	237	299	265	126	381
1961	235	290	267	111	312
1962	245	253	267	129	266
1963	148	135	156	130	220
1964	112	93	167	168	154
1965	124	152	161	102	203
1966	23	69	145	96	326
1967	0	138	121	135	241
1968	292	232	192	137	215

a Records not available.

between 87 and 173 metric tons and averaged 132 tons, and from 1955 to 1968 fluctuated between 156 and 381 and averaged 239 tons. The increased use of airplanes and other improvements in fishing methods, rather than any increases in the abundance of menhaden, probably were responsible for the large catches per vessel week in the later years.

While the catches per vessel week were lower for ports in the South Atlantic area than for ports in the Middle Atlantic, the variation between ports in each area was of about the same magnitude (Table 8). In the South Atlantic the figures for Southport and Fernandina Beach were about equal to each other but higher than for Beaufort. In the Middle Atlantic the catch per vessel week usually was highest at Tuckerton.

The monthly catch-per-vessel-week figures were computed for each area, but they showed no consistent trends or variation worth noting.

NUMBER OF PURSE-SEINE SETS

The number of purse-seine sets was estimated from logbooks and reduction plant records by the formula:

$$S_t = L_t(S_1/L_1)$$

where:

S_t = number of estimated monthly sets,
S_1 = number of sets from logbooks,
L_1 = number of days for which number of sets is known,
L_t = total number of landings days from plant records.

Vessels at each port were stratified by months and by loading capacity, on the assumption that the number of sets per day varied with both time and capacity. The number of monthly sets was estimated for vessels in each stratum.

TABLE 8.—Mean catch of Atlantic menhaden per vessel week, in metric tons, landed at ports in the South and Middle Atlantic areas.

Year	Fernandina Beach, Fla., and Yonges Is., S.C.	Southport, N.C.	Beaufort, N.C.	Lewes, Del.	Wildwood, N.J.	Tuckerton, N.J.	Port Monmouth, N.J.
1940	a	73	27	255	165	b	318
1941	106	88	36	292	211	b	257
1942	109	84	34	261	243	b	217
1943	170	119	51	337	309	b	344
1944	170	148	107	319	269	b	302
1945	134	164	97	331	309	198	256
1946	121	181	80	413	331	306	278
1947	73	180	103	382	234	343	252
1948	129	158	118	189	210	216	226
1949	78	207	110	238	200	213	186
1950	71	54	57	256	164	270	188
1951	193	82	70	266	140	279	233
1952	247	154	75	367	177	412	259
1953	140	98	75	444	505	524	374
1954	100	93	72	438	359	457	327
1955	85	107	80	404	333	433	258
1956	138	148	103	436	346	518	399
1957	86	104	73	301	255	368	377
1958	63	193	74	366	268	221	194
1959	194	161	70	301	253	252	273
1960	184	143	86	346	259	278	259
1961	157	132	64	332	259	258	258
1962	180	133	92	247	240	254	269
1963	149	108	127	115	150	137	155
1964	129	227	140	34	80	61	56
1965	105	137	69	131	103	b	187
1966	137	67	72	50	238	b	48
1967	173	172	192	b	171	b	122
1968	122	260	189	b	175	b	261

a Records not available.
b Plant closed.

Monthly totals at each port were obtained by summing the estimates for each stratum, seasonal totals by summing the monthly estimates, and area totals by summing the totals of each port. The mean number of sets per day for either month or season was calculated by dividing the total number of estimated sets by the total number of fishing days.

Because of the difficulty of maintaining good logbook records in recent years, the analysis was not continued beyond 1966. By that time little fishing was done north of Chesapeake Bay.

At ports where more than one size class of vessels fished, the larger vessels generally averaged slightly more sets per day than the smaller ones (Table 9). The differences were greater at ports where the vessel classes were not adjacent (Lewes and Wildwood) than they were at ports where the vessel classes were adjacent (Amagansett, Port Monmouth, and Tuckerton). Because data were insufficient to calculate the mean catch per set for each vessel class in Chesapeake Bay, the data were combined for classes 2 and 3, and 4 and 5. After 1964 the lack of data made meaningful comparisons impossible.

The slightly greater mean number of sets per day for the larger vessels may reflect the ability of these vessels to steam faster and range farther from their home port, and to carry more fish when fully loaded. More than likely, these figures reflect the ability and aggressiveness of the vessel captains, since the better ones generally are assigned to the larger vessels.

The annual or monthly number of sets (Table 10) reflected the abundance of fish and the amount of fishing effort. Excluding the North Carolina fall fishery, the most sets per season through 1963 were usually made in the Middle Atlantic area and the fewest sets in the South Atlantic. After 1963, following the drastic decline of the fishery and the decrease in effort in the Middle and North Atlantic areas, the number

TABLE 9.—Mean number of purse-seine sets per day, Atlantic menhaden fishery, by port and vessel class.

Year	Amagansett, N.Y.		Port Monmouth, N.J.		Tuckerton, N.J.		Lewes, Del.		Wildwood, N.J.		Reedville, Va.	
	Class		Class		Class		Class		Class		Class	
	5	6	5	6	5	6	3	5	2	5	2-3	4-5
1955	2.49	2.91	3.23	3.71	--	--	3.46	3.93	3.07	3.93	--	--
1956	2.82	2.88	3.43	4.03	4.41	4.68	3.38	3.98	3.15	3.99	--	--
1957	3.34	3.17	3.98	4.00	4.44	4.54	3.67	4.52	3.22	3.75	4.56	5.25
1958	2.63	2.83	3.26	2.71	2.78	3.67	3.79	3.07	--	--	4.12	3.76
1959	2.72	3.06	3.75	3.58	3.86	4.21	3.19	3.92	2.88	3.43	4.40	4.84
1960	2.79	2.81	3.69	3.54	4.29	4.57	--	4.84	3.61	3.96	3.86	4.38
1961	3.00	3.35	3.40	3.85	3.98	3.75	3.28	4.21	3.07	3.50	3.92	4.40
1962	2.78	3.29	3.49	3.85	3.49	3.61	3.53	3.46	2.74	3.09	2.86	3.42
1963	2.51	3.03	2.60	3.17	3.16	3.27	2.14	3.34	2.96	2.95	3.09	3.39
1964	2.30	2.91	2.41	2.65	--	3.85	--	--	--	--	2.95	3.62
Mean	2.74	3.02	3.32	3.51	3.80	4.02	3.31	3.92	3.09	3.58	3.72	4.13
Difference	0.28		0.19		0.22		0.61		0.49		0.41	

of sets in Chesapeake Bay, reflecting the increase in effort, was more than double the number in any other area.

There also were differences in the mean number of sets per day between areas (Table 11). Generally, the greatest number of sets per day was made in Chesapeake Bay, where vessels averaged about 0.10 set per day more than vessels in the Middle Atlantic. The fewest sets per day were made in the South Atlantic, where the tendency of schools to disappear by midday limited fishing to the forenoon, and in the North Carolina fall fishery, where the huge schools of fish enabled the vessels to load with relatively few sets.

CATCH PER SET

The mean catch per set varied monthly and annually in each area (Table 12). In all areas except the North Atlantic, it tended to be smaller during the middle part of the season than during the early or later part. In the Middle and North Atlantic areas, it averaged 9 tons more in October than in any other month. Annually, it fluctuated randomly in all areas except the Middle Atlantic, where it decreased after 1962.

Since purse seines tend to capture an entire school, the mean catch per set is an estimate of mean school biomass.

The school biomass appears to increase as the average age of the fish constituting the school increases. The catch per set in the North Atlantic, where 3-year and older fish constitute the bulk of catch, was higher than in the South Atlantic and Chesapeake Bay, where 1- and 2-year-old fish compose most of the catch (Nicholson and Higham, 1964). In the South Atlantic in 1960 and 1961, and in Chesapeake Bay in 1958, 1960, and 1961, when 2- rather than 1-year-old fish composed an unusually high percentage of the catch (Nicholson and Higham, 1964), the mean catch per set was relatively high. In the Middle Atlantic area in 1955 and 1956, when the catch contained a large percentage of fish older than age 2 (June and Reintjes, 1959, 1960), the mean catch per set was relatively high. Both the mean catch per set and the average age were low in the North Atlantic in 1957 and 1958. In the Middle Atlantic both the average age and the mean catch per set tended to decrease from June to September and then increase sharply in October, while in the North Atlantic both tended to increase from June to October.

Except for the South Atlantic area, where the disappearance of schools by midday limits the number of sets, the mean number of sets per day (Table 11) and the mean tons per set (Table 12) were inversely correlated, implying that fewer sets were necessary to load a vessel in areas where the school biomass was large, that schools became more numerous as their biomass decreased, or that heavy fishing pressure tended to keep school size small.

Relative abundance also appears to influence school biomass, but the relationship is not clear. When the catch per vessel week, a measure of

TABLE 10.—Estimated number of purse-seine sets in the Atlantic menhaden fishery, by year, month, and area.

Area	Year	Month							Total	North Carolina fall fishery
		Apr.-May	June	July	Aug.	Sept.	Oct.	Nov.		
South Atlantic and North Carolina fall fishery	1955	640	1,422	716	303	77	196	0	3,354	1,477
	1956	1,421	817	463	572	411	197	0	3,881	2,358
	1957	606	761	435	564	315	85	0	2,766	1,556
	1958	704	708	574	365	561	118	0	3,030	2,354
	1959	812	1,260	1,129	847	506	225	0	4,779	1,827
	1960	126	506	590	847	131	105	0	2,305	1,408
	1961	310	512	420	512	457	131	0	2,342	1,316
	1962	432	648	454	573	806	259	0	3,172	2,568
	1963	513	354	380	606	449	140	0	2,442	2,121
	1964	403	634	540	496	216	--	0	2,289	1,412
	1965	270	531	392	393	309	246	0	2,141	1,826
	1966	120	298	257	387	235	62	0	1,359	1,603
Chesapeake Bay	1955	--	--	--	--	--	--	--	--	
	1956	0	2,025	1,485	2,444	1,361	376	0	7,691	
	1957	0	2,697	2,501	2,880	2,292	762	0	11,132	
	1958	0	1,916	2,093	2,208	2,423	550	0	9,190	
	1959	0	3,060	3,036	2,914	2,657	1,328	0	12,995	
	1960	0	1,450	1,468	1,878	1,525	899	0	7,220	
	1961	0	2,376	1,713	1,874	1,257	802	0	8,022	
	1962	0	1,306	2,751	1,346	1,491	1,227	0	8,121	
	1963	0	2,150	1,374	1,567	1,411	979	0	7,481	
	1964	0	2,253	1,798	1,925	1,747	1,334	1,037	10,094	
	1965	0	1,927	1,137	1,912	1,633	1,533	795	8,937	
	1966	0	1,473	1,484	2,460	1,386	1,550	888	9,241	
Middle Atlantic	1955	0	3,857	3,483	2,693	2,304	920	0	13,257	
	1956	0	3,740	3,258	4,264	2,130	950	0	14,342	
	1957	0	3,589	3,991	4,637	2,641	2,045	0	16,903	
	1958	0	1,216	2,352	3,098	2,919	243	0	9,828	
	1959	0	2,884	3,496	3,184	2,448	805	0	12,817	
	1960	0	2,894	3,889	4,707	2,162	1,556	0	15,208	
	1961	0	3,529	3,780	5,085	2,233	888	0	15,515	
	1962	0	5,243	1,987	2,732	1,839	1,088	0	12,889	
	1963	0	3,086	1,952	2,083	1,025	618	0	8,764	
	1964	0	1,035	832	663	576	111	0	3,217	
	1965	0	1,083	733	937	432	152	0	3,337	
	1966	0	359	168	162	63	--	0	752	
North Atlantic	1955	0	647	1,319	881	413	198	0	3,458	
	1956	0	579	1,195	1,228	557	302	0	3,861	
	1957	0	590	1,435	1,332	689	340	0	4,386	
	1958	0	184	519	654	432	280	0	2,069	
	1959	0	350	1,085	996	764	265	0	3,460	
	1960	0	611	800	1,092	382	236	0	3,121	
	1961	0	584	750	1,259	403	269	0	3,265	
	1962	0	624	344	419	409	347	0	2,143	
	1963	0	453	422	624	301	217	0	2,017	
	1964	0	94	233	183	125	30	0	665	
	1965	0	171	190	198	150	0	0	709	
	1966	0	9	19	125	70	0	0	223	

abundance, declined drastically in the Middle Atlantic area in 1963, the mean tons per set also declined. But in the North Atlantic area, where the catch per vessel week also dropped sharply in 1963, the mean tons per set did not drop until 1965. Where the decline in the catch per vessel week was not so severe, no changes in the catch per set were noted. Perhaps population density must reach a rather low level before it can cause a significant decrease in school size. A factor which may contribute to an ostensible decrease in school size is selectivity by vessel captains, who have a tendency to pass by the smaller schools when fish are abundant. When fish are scarce, captains are less discriminate.

VARIATION IN ABUNDANCE

Atlantic menhaden are pelagic, but they rarely range far from shore. Most are caught within 20 miles of the coast. People have speculated that a large population, unavailable to the fishery,

TABLE 11.—Mean number of purse-seine sets per vessel day in the Atlantic menhaden fishery, by year, month, and area. Raw means are weighted, column means are unweighted.

Area	Year	Month							Mean	North Carolina fall fishery
		Apr.-May	June	July	Aug.	Sept.	Oct.	Nov.-Dec.		
South Atlantic and North Carolina fall fishery	1955	--	2.42	2.54	2.04	--	--	0	2.40	2.14
	1956	2.00	2.64	1.36	2.00	3.00	--	0	2.07	2.49
	1957	1.65	2.44	--	2.30	1.67	1.20	0	1.97	2.79
	1958	3.12	2.75	2.00	1.54	2.36	--	0	2.47	2.35
	1959	2.30	2.67	2.43	2.46	2.60	--	0	2.50	2.42
	1960	2.36	2.45	2.82	2.97	--	--	0	2.70	2.76
	1961	2.69	1.79	2.88	--	--	--	0	2.20	2.11
	1962	2.65	2.69	3.24	2.85	3.60	2.88	0	2.88	2.39
	1963	2.32	2.21	2.50	3.00	3.40	3.50	0	2.41	2.62
	1964	2.25	2.43	2.40	2.35	2.63	--	0	2.41	2.60
	1965	1.71	2.39	2.23	1.90	2.32	3.33	0	2.17	2.78
	1966	1.72	2.24	1.95	2.51	2.06	2.00	0	2.09	2.76
	Mean	2.25	2.43	2.40	2.36	2.62	2.58	0	2.36	2.52
Chesapeake Bay	1955	--	--	--	--	--	--	--	--	
	1956	0	3.70	3.49	3.98	3.82	3.33	0	3.72	
	1957	0	4.43	4.81	4.72	4.89	3.10	0	4.56	
	1958	0	3.45	3.89	4.08	5.08	2.85	0	3.99	
	1959	0	4.13	4.10	5.32	5.27	3.73	0	4.50	
	1960	0	3.82	4.19	3.95	4.34	3.72	0	4.00	
	1961	0	4.57	4.00	3.68	3.65	3.48	0	4.01	
	1962	0	2.93	3.15	3.30	2.76	2.71	0	2.98	
	1963	0	3.75	2.34	2.82	3.20	3.69	0	3.25	
	1964	0	3.21	3.00	3.75	3.63	3.09	4.03	3.38	
	1965	0	3.22	2.69	3.08	2.88	3.31	4.07	3.06	
	1966	0	2.67	2.92	3.53	2.79	3.05	3.07	3.03	
	Mean	0	3.62	3.51	3.84	3.85	3.28	3.72	3.68	
Middle Atlantic	1955	0	3.38	4.15	3.83	3.38	2.68	0	3.61	
	1956	0	3.79	4.17	4.40	3.51	2.41	0	3.87	
	1957	0	3.50	4.50	4.67	4.03	3.21	0	4.07	
	1958	0	2.63	3.19	3.41	3.89	2.53	0	3.33	
	1959	0	3.30	3.93	4.16	3.45	2.65	0	3.68	
	1960	0	4.22	4.68	4.51	4.00	2.89	0	4.26	
	1961	0	3.24	4.04	4.48	3.68	2.96	0	3.82	
	1962	0	3.84	3.03	4.21	3.15	2.12	0	3.45	
	1963	0	3.15	3.13	3.30	3.20	1.96	0	3.07	
	1964	0	2.41	3.19	3.56	3.01	--	0	2.98	
	1965	0	3.35	3.28	4.01	2.78	3.62	0	3.40	
	1966	0	2.79	--	3.95	2.75	--	0	3.08	
	Mean	0	3.30	3.75	4.04	3.40	2.70	0	3.55	
North Atlantic	1955	0	2.49	3.23	2.45	1.98	2.28	0	2.48	
	1956	0	2.63	2.89	3.41	2.53	2.25	0	2.84	
	1957	0	3.80	3.55	2.96	2.89	2.97	0	3.28	
	1958	0	2.13	2.93	2.83	2.66	2.37	0	2.70	
	1959	0	2.14	2.53	3.46	2.60	1.97	0	2.73	
	1960	0	2.70	2.74	3.64	2.07	2.11	0	2.79	
	1961	0	2.75	3.24	3.77	2.54	2.60	0	3.12	
	1962	0	3.06	2.77	3.56	2.73	2.61	0	2.96	
	1963	0	2.54	3.42	2.96	2.61	1.67	0	2.75	
	1964	0	1.87	3.26	2.48	2.33	1.92	0	2.58	
	1965	0	2.87	2.96	2.54	2.39	--	0	2.71	
	1966	0	1.40	2.78	5.00	--	--	0	2.24	
	Mean	0	2.53	3.03	3.26	2.48	2.28	0	2.77	

may occur far offshore. There is no available evidence to support this view.

There is evidence, however, that the entire population is fished. Since 1945 Atlantic menhaden have been exploited from northern Florida to the Gulf of Maine, an area constituting nearly their entire range. With the advent of airplanes that could search larger areas and vessels that could range up to a hundred miles from port, no areas have been unsearched or unfished, except where prohibited by local restrictions.

Under these conditions changes in the catch per unit of effort are assumed to reflect changes in actual, rather than apparent, abundance. Even though the figures have been influenced by changes in vessel efficiency, they are sensitive

TABLE 12.—Mean catch per purse-seine set of Atlantic menhaden, in metric tons, by year, month, and area. Row means are weighted, column means are unweighted.

Area	Year	Month						Mean	North Carolina fall fishery
		Apr.-May	June	July	Aug.	Sept.	Oct.		
South Atlantic and North Carolina fall fishery	1955	16.4	11.9	11.3	7.4	15.9	16.9	12.6	44.4
	1956	19.4	21.9	16.1	12.7	13.6	13.6	17.7	31.2
	1957	10.7	17.3	14.5	10.0	12.2	11.1	13.1	35.6
	1958	10.4	15.3	21.4	8.4	9.1	21.4	13.5	29.8
	1959	16.8	16.9	11.2	10.0	9.5	9.7	13.2	44.8
	1960	13.2	12.0	13.8	16.5	13.0	48.7	16.0	44.2
	1961	22.6	24.9	15.4	14.6	17.9	15.3	18.6	53.3
	1962	14.2	15.3	12.4	16.4	9.3	13.4	13.2	45.5
	1963	16.4	18.5	18.9	13.4	7.5	3.2	14.0	28.3
	1964	25.6	22.5	23.6	15.5	3.6	--	20.0	27.6
	1965	17.4	25.7	17.2	15.0	10.7	10.3	17.2	28.8
	1966	20.2	15.3	19.2	18.4	21.1	12.3	18.2	44.7
	Mean	17.0	18.1	16.2	13.2	12.0	16.0	15.6	38.2
Chesapeake Bay	1955	--	--	--	--	--	--	--	
	1956	--	12.6	14.3	10.8	12.9	9.1	12.2	
	1957	--	11.8	11.9	9.6	13.1	11.1	11.4	
	1958	--	11.9	20.7	18.9	16.0	8.8	16.4	
	1959	--	15.3	13.2	14.8	16.0	18.1	15.2	
	1960	--	21.8	14.2	14.1	11.2	14.0	15.1	
	1961	--	16.1	20.0	12.2	16.9	11.1	16.1	
	1962	--	29.1	15.2	16.9	13.2	23.6	18.5	
	1963	--	12.9	16.2	15.8	12.4	11.9	13.9	
	1964	--	14.2	13.4	13.3	9.3	15.3	13.2	
	1965	--	15.9	15.7	13.6	11.9	13.0	13.9	
	1966	--	11.9	11.7	8.4	10.5	13.8	12.6	
	Mean	--	15.8	15.1	13.5	13.1	13.6	14.4	
Middle Atlantic	1955	--	23.0	23.8	21.3	23.3	37.4	24.0	
	1956	--	29.1	25.7	25.6	22.2	30.7	26.4	
	1957	--	16.5	18.4	15.5	14.6	30.0	18.0	
	1958	--	18.1	19.1	24.0	22.7	15.0	21.5	
	1959	--	22.8	18.1	18.8	16.6	26.1	19.6	
	1960	--	15.6	17.3	16.2	15.3	21.7	16.8	
	1961	--	19.4	22.8	15.2	12.7	15.5	17.7	
	1962	--	22.6	16.8	8.3	15.1	48.7	19.8	
	1963	--	17.2	9.5	6.3	10.1	16.5	12.7	
	1964	--	10.7	10.8	13.3	11.2	11.0	11.3	
	1965	--	13.0	10.2	14.2	17.1	27.2	13.7	
	1966	--	7.0	4.7	10.3	16.3	--	8.0	
	Mean	--	18.0	16.4	15.8	16.4	25.4	17.4	
North Atlantic	1955	--	12.9	21.2	31.2	26.9	41.6	24.0	
	1956	--	23.2	24.4	25.1	26.8	33.9	25.5	
	1957	--	17.7	15.4	18.1	24.1	29.6	19.1	
	1958	--	14.4	10.5	16.9	18.6	16.7	15.4	
	1959	--	19.5	18.9	18.9	17.1	26.0	19.0	
	1960	--	24.3	19.2	18.8	19.8	34.7	21.2	
	1961	--	14.3	19.5	18.9	16.7	24.9	18.0	
	1962	--	22.9	21.3	17.6	22.8	44.7	25.1	
	1963	--	18.6	9.4	20.1	19.7	19.9	17.4	
	1964	--	22.8	30.2	19.3	23.8	34.3	25.1	
	1965	--	13.2	14.3	20.8	18.5	--	16.7	
	1966	--	4.4	4.3	8.5	9.5	--	8.3	
	Mean	--	17.3	17.4	19.5	20.3	30.6	19.6	

enough to reflect real differences in population abundance.

Variations in year-class strength have contributed to fluctuations in population abundance. Estimates of year-class strength prior to 1952 have been based on catch-per-unit-of effort figures and since 1952 on catch samples. From 1950 to 1958 there were four exceptionally large year classes, the largest occurring in 1958 (June and Reintjes, 1959; Nicholson and Higham, 1964). Most of the year classes after 1958 have been smaller than any of the year classes prior to 1958. This series of small year classes occurred simultaneously with the general decline in abundance, which began about 1956 and became more noticeable in 1963, after the large

1958 year class had nearly passed from the fishery.

The greatest decline in abundance has been in the Middle and North Atlantic areas, where older fish constitute the bulk of the catches. Fish pumps and airplane spotters, two of the improvements having the most impact on fishing effectiveness, increased sharply in both areas after 1949. Yet the catch per vessel week, after reaching a peak in about 1952, declined thereafter in both areas, despite other fishing improvements added in the middle 1950's. In the North Atlantic, the catch per vessel week, except for 1952 and 1953, was no greater from 1950 through 1962 than it had been from 1941 to 1950. In the Middle Atlantic, the catch per vessel week, although being substantially greater from 1952 to 1962 than it had been up until 1951, began a steady decline in 1957, and from 1963 to 1966 was much lower than in the years prior to 1950. From these data one may conclude that the abundance of menhaden in these two areas was no greater from 1950 to 1962, and considerably less after 1962, than it had been prior to 1950.

The decline in abundance in Chesapeake Bay, where 1- and 2-year-old fish compose most of the catches, has not been as great as in the North and Middle Atlantic. The catch per vessel week was substantially greater from 1954 to 1962 than it was prior to 1954 or after 1962. Since the major improvements in fishing methods came a few years later than in the Middle and North Atlantic, the higher catches per vessel week after 1953 probably reflect an increase in fishing efficiency, although they could reflect an increase in menhaden abundance. The decrease after 1962 probably resulted from a true decrease in menhaden abundance.

Abundance in the South Atlantic, where age-1 fish compose most of the catch, appears to have remained unchanged. The catches per vessel week varied widely, but showed no trend. In this area the fisheries at the three ports are small, geographically distinct, and dependent on relatively small numbers of fish, principally of one age group, that are dispersed over a large area. If the carrying capacity is less in the South Atlantic than in other areas, the abundance of fish in the area is less likely to reflect changes in the total Atlantic menhaden population than is the abundance of fish in areas of high density and high carrying capacity, such as Chesapeake Bay.

In the North Carolina fall fishery menhaden nearly always will appear to be abundant, because they are concentrated in a small area for a short period of time and are easy to catch. But since weather is more variable than in other areas, it influences the catch per vessel week more than it does elsewhere. The wide fluctuations in the catch per vessel week, therefore, do not necessarily reflect variations in abundance.

The relation between the decline in abundance and the high levels of fishing effort can be understood only if the spawning age, the age and size distribution, and the seasonal movements of the fish are considered. Atlantic menhaden spawn after they have completed three growing seasons (Higham and Nicholson, 1964), and rarely survive past seven growing seasons. Their age and size distribution and seasonal movements have been described by June and Nicholson (1964) and Nicholson,[2] and are briefly summarized here.

During the fishing season from about May to October, the population from Florida to Chesapeake Bay is composed primarily of age-1 and age-2 fish. Although the proportion of each age group varies with the strength of individual year classes, age-1 fish are usually more abundant, particularly south of Cape Hatteras. From the mouth of Chesapeake Bay to Long Island, age-2 fish gradually replace age-1 fish as the dominant age group. Age-3 fish, dominant in Long Island and Nantucket Sounds, become less abundant north of Cape Cod, where age-4 to age-7 fish predominate. A southward movement begins among fish at the northern end of the range in late summer and extends to all fish north of Cape Hatteras by early November. By mid-January nearly all menhaden have moved into the offshore area between Cape Lookout and northern Florida. In late winter these fish begin a northward movement.

[2] Nicholson, William R. Movements of Atlantic menhaden as inferred from changes in age and size distribution. (Unpublished manuscript.)

As older fish decreased in abundance, fisheries dependent on them declined. No menhaden were landed after 1958 at Portland, after 1962 at Gloucester, or after 1963 at Point Judith. After the 1958 year class ceased to contribute large numbers to the catch, the Amagansett, Port Monmouth, and Tuckerton catches dropped sharply. As catches declined and plants closed or reduced fishing, effort also dropped. By 1968 only 136 vessel weeks were expended in the North and Middle Atlantic, as compared with 1,265 in 1962.

Effort in areas where age-1 and -2 fish were predominant continued to be high. In 1968, 846 vessel weeks were expended in the South Atlantic and Chesapeake Bay, as compared with 909 in 1962.

Changes in the catch and the catch per vessel week suggest that the decline in numbers of fish older than age 2 was much greater than the decline in numbers of fish younger than age 3.

If recruitment is dependent on spawning population size, and spawning population size is dependent on the escapement of prespawning age fish, the total yield will be limited by the amount of escapement. Schaaf and Huntsman[3] have shown that with present levels of fishing effort, the spawning stock of Atlantic menhaden is inadequate for recovery of the population.

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ABUNDANCE AND DISTRIBUTION OF YOUNG ATLANTIC MENHADEN, *Brevoortia tyrannus,* IN THE WHITE OAK RIVER ESTUARY, NORTH CAROLINA

E. Peter H. Wilkens[1] and Robert M. Lewis[2]

ABSTRACT

The effect of salinity, temperature, tide, turbidity, and illumination on the distribution of larval, prejuvenile, and juvenile menhaden in an estuary was investigated. Most menhaden larvae entered the estuary in March after the water had warmed to about 10° C, and moved upstream to the low-salinity-freshwater zone where they transformed into juveniles. More larvae were caught in the lower estuary on flood tide. After transformation to juveniles they were caught in schools throughout the estuary. Turbidity and illumination did not affect the distribution of menhaden, but illumination affected catchability, since more menhaden were collected during night tows.

In this study we investigated the effects of temperature, salinity, and light on the distribution and abundance of larval, prejuvenile, and juvenile menhaden in a single estuary, the White Oak River in North Carolina. As the strength of individual year classes of Atlantic menhaden fluctuates widely, we were interested in determining what effect these environmental factors had on menhaden during their first year in an estuary. This information could be helpful in assessing and predicting the strength of individual year classes. Estimates of the strength of individual year classes before they enter the fishery would be valuable to the commercial fishery. A single estuary was selected so that a better understanding of these variables could be achieved before being applied to a coastwise fishery.

Atlantic menhaden, found along the eastern coasts of the United States and Canada from Nova Scotia to southern Florida (Hildebrand, 1964; Reintjes, 1964), spawn in almost every month in some part of their range (Higham and Nicholson, 1964). Menhaden are spawned in the ocean and enter an estuary as larvae. Once strong enough to swim against the tidal currents, they move upstream towards fresh water (Lewis and Mann, 1971) where they transform into juveniles. They remain in the estuary for their first growing season, gradually moving downstream in the summer and reaching the lower estuary or open sea by autumn (June and Chamberlin, 1959; Massmann, Ladd, and McCutcheon, 1954).

STUDY AREA, SAMPLING LOCATIONS, PROCEDURES, AND NETS

The White Oak River estuary is a bar-built estuary (Pritchard, 1967) which drains forest lands in the upstream part and salt marshes in the downstream part (North Carolina State Board of Health, 1954). The Intracoastal Waterway crosses the mouth of the estuary near Bogue Inlet.

We selected this estuary because: (1) We knew from preliminary sampling that larval menhaden entered the lower section from the ocean in the winter and early spring and that juveniles occurred in the upper section in the summer; (2) its small size (28 sq km) permitted ample sampling coverage; and (3) its proximity to the Beaufort laboratory made frequent sampling easy.

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We assumed that few or no larvae moved from other estuaries into the White Oak River estuary.

We collected larval, prejuvenile, and juvenile menhaden at 14 sampling locations extending 34 km upstream from Bogue Inlet (Figure 1). The distance between stations varied from 2 to 5 km and averaged about 3 km. The type of gear we used, frequency of sampling, and date of sampling are listed in Table 1.

TABLE 1.—The White Oak River estuary sampling schedule.

Sampling location	Sampling frequency	Gear	Sampling period
Swansboro Bridge (Station 2)	2-3 days/week	Channel net	Nov. 1967-Apr. 1968
			Nov. 1968-Apr. 1969
Upstream stations 6-12	Monthly	Surface trawl	July-Sept. 1968
Upstream stations 6-12	Weekly	Channel net	Feb.-Apr. 1969[1]
Upstream stations 6-12	Biweekly	Channel net	May 1969
Upstream stations 6-12	Monthly	Channel net	June-Sept. 1969[2]

[1] Stations 1, 3, 4, and 5 were sampled irregularly in this period.
[2] A few samples were taken upstream with the surface trawl in this period.

We sampled larvae entering the estuary at the Swansboro Bridge (station 2) 2 or 3 days per week from November through April in 1967-68 and 1968-69. During July, August, and September 1968, we sampled at several of the upstream stations. Starting in February 1969 we collected menhaden throughout the river and estuary, although our efforts were concentrated on the upstream section (stations 6 through 12). In March and April we visited these stations every week; in May, every 2 weeks; and from June to September, every month.

During the 1967-68 and 1968-69 seasons, we sampled for larvae with a channel net described by Lewis, Hettler, Wilkens, and Johnson (1970). The net, with a 1 by 3 m opening, had a tail bag constructed of 0.5-mm mesh. At Swansboro we attached the net to the bridge and made four to six 30-min sets per day. At the other locations, we towed the net between two 16-ft aluminum boats and made a 15-min set when the larval and prejuvenile menhaden were scarce and a 5-min set when they were abundant.

During July, August, and September 1968, we sampled juveniles with a 6.1-m surface trawl having a 6.2-mm bar mesh. We towed it in the same manner as the channel net. During the corresponding months in 1969, most of the collections were made with the channel net.

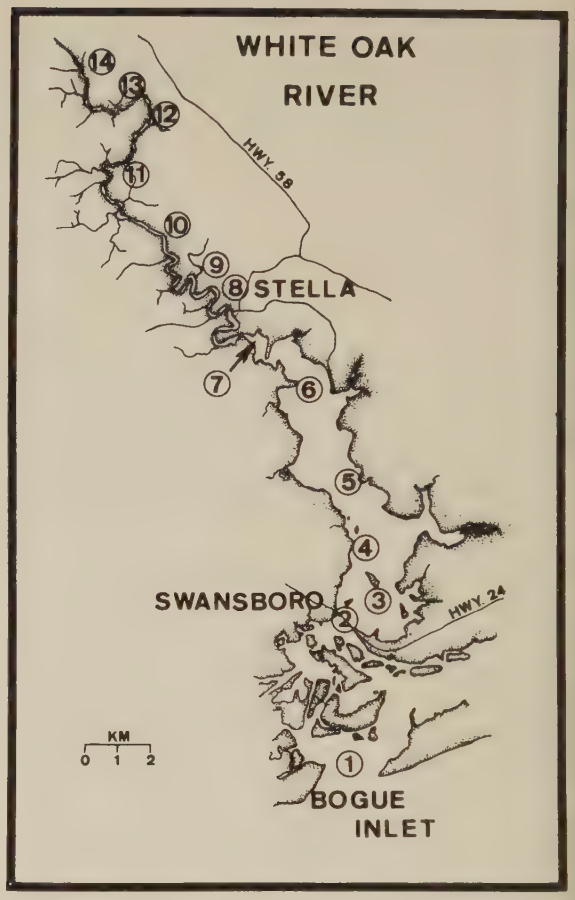

FIGURE 1.—Sampling locations for young menhaden on the White Oak River estuary, N.C.

In all the collections, the number of menhaden caught was expressed as an index (I = number of young menhaden per 100 m^3 water strained).

We recorded surface temperature and salinity at the start and end of each set at the bridge and at the end of each tow at the other sites. We measured the amount of water strained by the net during each set with a flowmeter. Dissolved oxygen and turbidity readings were taken only in July, August, and September 1968.

TEMPORAL DISTRIBUTION

Larval menhaden entered the White Oak River from November until early May. Two peaks of abundance occurred each year, one in November and December and the second and major peak in February and March (Figure 2).

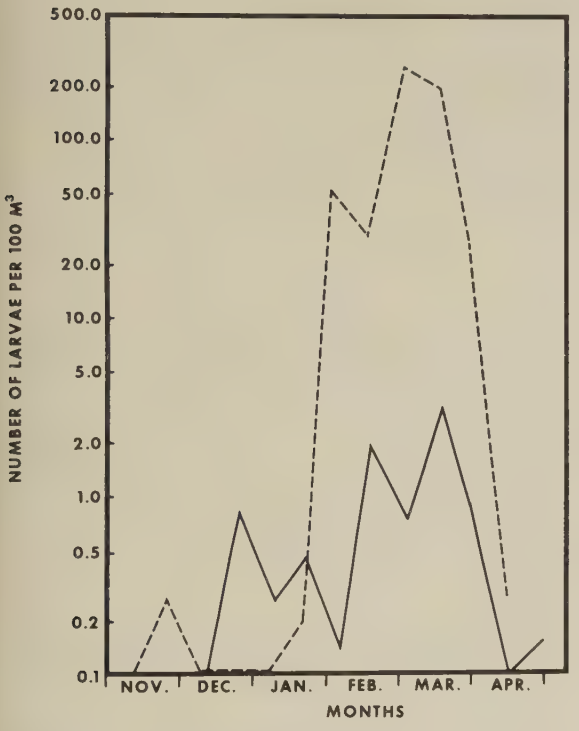

FIGURE 2.—The mean biweekly abundance indexes at Swansboro Bridge in 1967-68 (solid line) and 1968-69 (dashed line).

The entrance of large numbers of larvae in February and March probably resulted from the migratory schools of menhaden that spawned off the North Carolina coast during the winter. Higham and Nicholson (1964) found that during November and December most of the females in the landings were nearly ripe. Reintjes (1969) reported finding hundreds of thousands of developing menhaden eggs off the North Carolina coast in December 1966.

Those larvae that entered the estuary during November and December were probably the progeny of fish that either had inhabited North Carolina waters in the summer or had moved into North Carolina waters from other areas in early autumn.

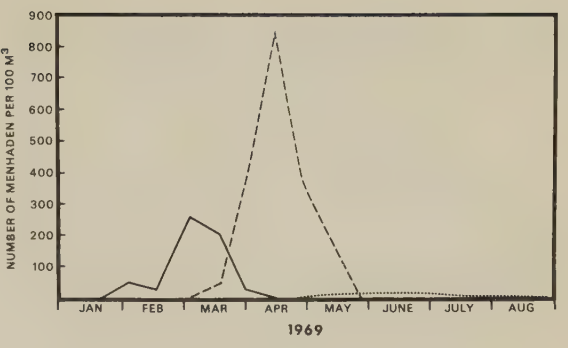

FIGURE 3.—The relative abundance of larval (solid line), prejuvenile (dashed line), and juvenile menhaden (dotted line) in the White Oak River estuary. (The larval indexes are from the bridge, and the prejuvenile and juvenile indexes are from the upstream zone where the fresh and salt water mix. Larval and prejuvenile indexes are biweekly means, but the juvenile index is a monthly mean plotted on the day the sample was obtained.)

Prejuvenile menhaden were first caught in March and became abundant in late March and April (Figure 3). After the peak in April the number of prejuveniles decreased, and by the beginning of May most had transformed into juveniles.

Juvenile menhaden, collected in relatively low numbers from May until September, occurred with maximum abundance in late May and June. As young menhaden got above 45 mm fork length during the summer of 1968, we caught fewer fish during the day. To determine if illumination was a factor that resulted in greater net avoidance by juvenile menhaden, we scheduled a series of day-night sampling trips. We collected larger samples of menhaden during nighttime tows, which indicated that some fish were able to avoid our net during the day. Fish from day and night tows were similar in length. In addition, we caught more menhaden on overcast or moonless nights than on clear, moonlight nights. As a result of our findings in 1968, we sampled for juveniles in 1969 only at night in order to increase our sampling efficiency.

EFFECT OF SALINITY, TEMPERATURE, AND TIDE ON THE DISTRIBUTION OF YOUNG MENHADEN

SALINITY

Larval menhaden, after entering the lower estuary, move upstream into lower salinities to metamorphose. They seek the zone of the river from 1 ‰ salinity to fresh water. This zone extends a short distance upstream from the interface between fresh and salt water. Larval and prejuvenile menhaden were most abundant in this zone where metamorphosis occurs (Figure 4). They apparently range into fresh water for only a short distance since they were absent or present only in small numbers in our samples farther upstream.

After the menhaden have transformed from prejuveniles to juveniles, they appear to seek higher salinity water. In late May when most of the prejuveniles had metamorphosed, we found juveniles in low-salinity water. As the season progressed the juveniles were present in the low-salinity water upstream, but they tended to be more abundant in water downstream. Schools of juvenile menhaden generally moved out of the estuary in the fall.

Both the position and length of the upstream zone where young menhaden concentrated are influenced by tidal excursion, rainfall, and wind direction and strength. A northeast wind causes unusually high tides and pushes salt water farther upstream than during normal flooding and ebbing tides.

We do not understand why low-salinity water is important to young menhaden, but one explanation is that they cannot metamorphose properly in either fresh or high-salinity water. When larvae were held in salinities ranging from 15 to 40 ‰, about one-third of the fish in each salinity group developed abnormalities of the spine (Lewis, 1966). Juveniles may also congregate in low-salinity areas at times because food may be more abundant.

In some estuaries turbidity may vary with salinity. We measured the turbidity at the Swansboro site in March, April, and May 1968 and at our upstream sites during the summer of 1968 to determine if it affected the number of young menhaden caught by our net, and to see if there was any relation between salinity and turbidity. At Swansboro, where the water remained relatively clear (light transmittance ranged from 89 to 96%), no correlation existed between turbidity and the catch of larvae. At our upstream tow areas, where the water also was clear, light transmittance ranged from 68 to 95%. We also found no relation between turbidity and catch of young menhaden. We concluded therefore that turbidity was too low to affect catchability in the White Oak River. As there were no marked differences between up- and downstream turbidities, we concluded also that there was no relation between salinity and turbidity.

TEMPERATURE

Larval menhaden are sensitive to low temperatures, particularly if the salinities are high or low. They have the best chance for survival in an estuary if the temperature remains above 4° C and the salinity ranges between 10 and 20 ‰ (Lewis, 1966). Below 4° C they survive for only a short time. Lewis (1965) determined that the number of hours to 50% mortality at 2.0° C varied from 3.2 to 38.5 hr depending on the acclimation temperature.

We compared the temperatures in the estuary during the 2-year study with temperature tolerances of larval menhaden determined in the laboratory by Lewis (1965, 1966). The water temperature in the White Oak River went below 4° C for several days in January and December 1968 and January 1969. Except for two sampling days in 1968 and one in 1969, the water temperature did not get over 10° C from the beginning of January to mid-March; it stayed at 2° C for 2 days during this period in 1968, and 1 day in 1969. We caught few menhaden larvae during the periods of low water temperature.

Most larvae that enter the estuary before the lethal cold water temperatures in the winter probably do not survive, while those that enter during the late winter and early spring probably remain in the downstream area because of the colder water upstream. As the water warms in the spring to above 10° C they move towards

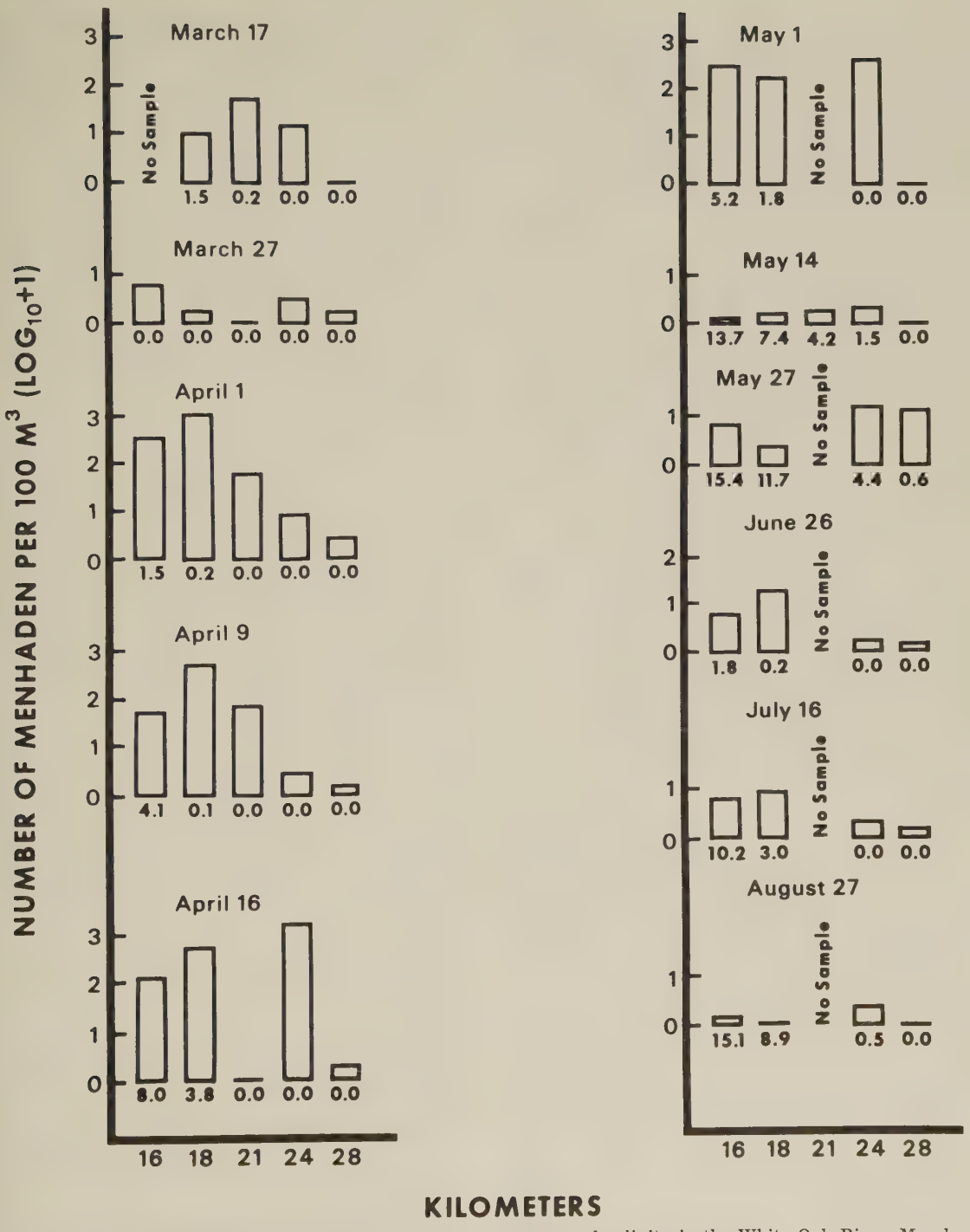

FIGURE 4.—The distribution of menhaden by date, kilometer, and salinity in the White Oak River, March-August 1969. (Number below each bar is salinity at station.)

the low-salinity freshwater zone. Those that enter later in the season, after the water has warmed, move upstream in a shorter time. Once menhaden had moved upstream, salinity and food supply probably affected their distribution more than temperature.

Since dead menhaden larvae do not float, we probably would not notice if kills occurred when the temperature dropped below 4° C. However, we did observe many dead young and adult bay anchovy (*Anchoa mitchilli*) and pinfish (*Lagodon rhomboides*) floating on the surface on January 10 and 12, 1968, when the water temperature was 2° C. Some of the floating fish revived when placed in warmer water, but most did not. We assume that many of the species present in the estuary either died from or were subject to cold stress. Thus any cold weather that occurs during the time larval fish are present in the estuary can have an important effect on the number of individuals surviving in the population.

Although high water temperature does kill juvenile menhaden, it did not appear to cause any mortality in the White Oak River estuary. In laboratory tests, juvenile menhaden died in water temperatures above 33° C (Lewis and Hettler, 1968). In the White Oak River the temperature remained below 33° C except for a short period when it rose to 34.1° C.

TIDE

Velocity of water current affects the abundance and distribution of fish larvae in an estuary. Bishai (1959) found that herring larvae (6-8 mm total length) maintained themselves in a current of 0.58 to 1.03 cm/sec and that at higher velocities they drifted with the current but at a rate less than the current.

During our sampling in the field we noticed that larval menhaden also held their positions only in weak currents. The menhaden larvae collected at the Swansboro bridge were larger (10-30 mm total length) than the herring tested by Bishai and seemed able to maintain their position at velocities less than 10 cm/sec. Above this velocity they were carried by the current. One would expect, therefore, to obtain large larval indexes during peak tidal flows at midflood and at early ebb. Larval indexes during these periods varied considerably, but in general were larger than indexes during late ebb and early flood tide stages (Table 2). The variability in abundance indexes arises, in part, from day-to-day changes in menhaden distribution in the lower estuary during the 2-month period. A 24-hr study in March 1968 at Beaufort, N.C., showed that larval abundance varied with the tide, current, and time of day (Lewis and Wilkens, 1971).

TABLE 2.—Number of menhaden larvae per 100 m^3 of water at hourly flood and ebb-tide stages, Swansboro, N.C., February-March 1969.

Stage	Hour	Mean velocity	Abundance index	Range	Number of collections
		m/sec			
Flood	1	0.10	33.6	17.2- 45.2	3
	2	0.17	216.0	16.0- 591.4	4
	3	0.15	94.9	0.8- 578.4	8
	4	0.18	74.0	4.0- 338.8	7
	5	0.15	894.9	1.5-3,582.0	7
Ebb[1]	1	0.22	65.6	20.6- 110.6	2
	2	0.27	168.0	25.6- 365.4	3
	3	0.23	43.1	7.2- 121.1	5
	4	0.21	26.4	0.4- 90.5	6
	5	0.19	17.8	2.2- 82.9	7
	6	0.16	6.5	1.9- 13.0	8
	7	0.11	8.7	1.4- 14.4	7

[1] The ebb-tide stage generally lasted about 2 hr longer than flood.

Tides affect the movement of larvae in and out of an estuary as well as within an estuary. Flooding currents carry larval menhaden into the estuary where, before heading upstream, they move back and forth with the changing tides. At the Swansboro bridge station more larvae were caught on flood tide than on ebb. During February and March 1969, larval indexes greater than 10 occurred in 81% of the sets made on flood tide but only in 51% of the sets on ebb tide. June and Chamberlin (1959) reported similar results at Indian River, Del. Some of the larger catches of the season occurred on late flood. The early hours of ebb tide had higher larval indexes than late ebb. As more larvae enter than leave, the number of larvae in the estuary reaches a maximum by midspring.

Tidal stage and current velocity affected the catchability of larvae. In the lower estuary these forces either concentrated the larvae in one location or spread them over a large area. In the upper estuary the location and width of the low-

salinity-freshwater zone, which was influenced by the tide, affected the distribution of larvae and prejuveniles.

SUMMARY

Larval menhaden were present in the White Oak River estuary from November to May but were most abundant in February and March. Prejuveniles were abundant in late March and April, and by the beginning of May most had transformed into juveniles. Our largest catches of juveniles occurred in May.

Larvae progress upstream to the zone where the salt and fresh water mix (0-1 ‰ salinity). Large catches of prejuvenile and larval menhaden occurred within this zone. We did not find juvenile menhaden in the zone until the end of May when most prejuveniles had transformed to juveniles.

Laboratory tests from other studies showed that menhaden died when the water temperature fell below 4° C and rose above 33° C. Even though young menhaden encountered both extremes of water temperature in the White Oak River, we saw no evidence of any deaths.

Catches of larval menhaden at the Swansboro bridge were more abundant on flood tide than ebb. The early hours of ebb tide had higher larval indexes than late ebb.

Illumination affected the catches of juvenile menhaden at our upstream stations as we caught more menhaden on overcast or moonless nights than on clear, moonlight nights or during the daylight hours.

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Isistius brasiliensis, A SQUALOID SHARK, THE PROBABLE CAUSE OF CRATER WOUNDS ON FISHES AND CETACEANS

EVERET C. JONES[1]

ABSTRACT

Evidence is presented that bites inflicted by the small squaloid shark, *Isistius brasiliensis* (Quoy and Gaimard), are the causes of crater wounds, crescentic wounds, and related scars on large pelagic fishes and cetaceans. This evidence consists of a crescentic "wound" experimentally produced on the side of a dead fish by a living *Isistius*; specialized morphology of the shark's basihyoid cartilage and coracohyoideus muscles, lips, labial cartilages, and spiracles, that, together, enable the shark to form an oral vacuum on a smooth surface; an experiment in which a living *Isistius* formed such a vacuum; specialized morphology and arrangement of the mandibular teeth; close agreement between the range of reported wound widths and the estimated range of bite widths of *Isistius;* agreement between the geographical ranges of *Isistius* and those fishes and cetaceans which bear crater wounds; and, finally, the presence in *Isistius* stomachs of hemispheroidal plugs of fish flesh. Speculation on the circumstances that may enable a small, slow shark to make contact with large, swift fishes and cetaceans is included. *Isistius* apparently qualifies as a temporary parasite.

Probably the earliest account of the existence of small, round or oval, scooped-out wounds on the sides of large pelagic fishes is contained in an ancient legend of Samoa (A. Utu, personal communication), which states that atu (skipjack tuna, *Euthynnus pelamis* (Linnaeus)) entered Palauli Bay, and, upon approaching the beach, left small round pieces of their flesh as gifts to Tautunu, chief of that community. Evidence of this sacrifice was found by the people who caught the atu and observed fresh, round wounds on their sides.

This legend provides one of many explanations that have been advanced regarding the causes of such wounds on large pelagic fishes as well as on whales and porpoises. This paper presents evidence that many crater wounds, crescentic wounds, and the resulting scars on pelagic fishes (Figure 1), and open pit wounds and resulting scars on cetaceans are the results of bites inflicted by the small squaloid shark, *Isistius brasiliensis* (Quoy and Gaimard). (A second species, *Isistius plutodus,* was described by Garrick and Springer (1964) from the Gulf of Mexico. Although nothing is known of the behavior of this species, which is based on one specimen, it is probable that its feeding habits are similar to those of *I. brasiliensis.*)

Such wounds on fishes have been reported by Nemoto (1955), Iversen (1959), Guitart M. (1964), Klawe (1966), Bane (1969), and Machado Cruz (1969). The literature on open pit wounds and related scars on cetaceans is much more extensive, apparently beginning with the work of Collett (1886). Mackintosh and Wheeler (1929) and van Utrecht (1959) presented thorough discussions of these wounds and probable causes, and summarized the previous literature. Nemoto (1955) noted that some of the wounds observed on whales are similar to and probably have a common origin with those on fishes. He further stated that a cause other than lamprey attacks, the most commonly advocated agent, must be found to account for crescent-shaped scars and open pit wounds on cetaceans and fishes.

It was not always possible for me to determine whether published photographs and descriptions were of wounds and scars of the types which I attribute to *Isistius* bites. I have never seen wounds known to have been produced by lampreys and therefore cannot comment with any

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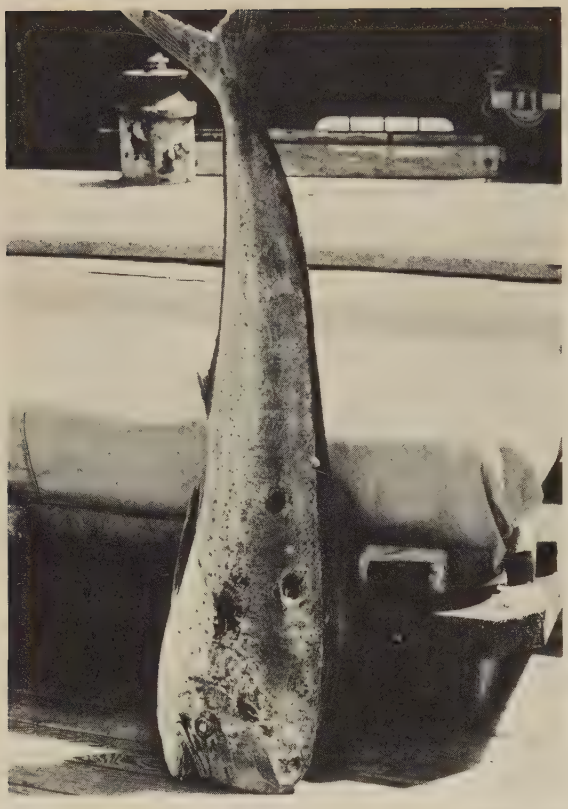

FIGURE 1.—Crater wounds on a large dolphin from the central Pacific.

authority on them. I believe, however, that Pike (1951) unknowingly but accurately described the differences between lamprey bites and *Isistius* bites on whales when he wrote: "The lampreys seem to leave two distinct types of wounds . . . . The first consists of a circular area in which the epidermis is completely abraded by the teeth of the sucking disc. In the center of this is a hole through the skin caused by the rasping tongue. In the other type the lamprey apparently rasps away the skin over the entire area with the result that there is a circular sore right down to the blubber and no periphery of skin which has been damaged but not eaten away." The second type and some of the wounds and scars illustrated by Pike are, I believe, attributable to *Isistius* bites.

Crater wounds have been reported in the literature cited on skipjack tuna; yellowfin tuna,

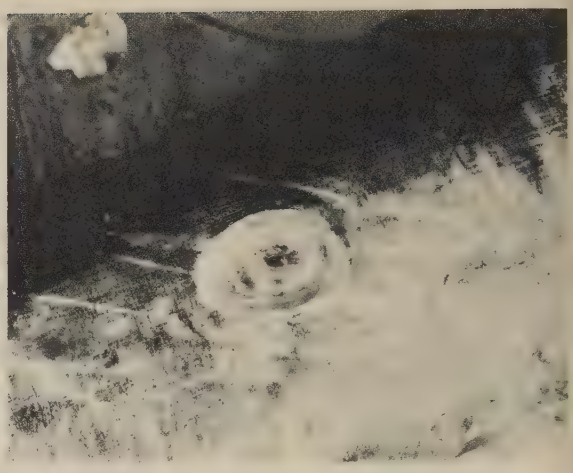

FIGURE 2.—A crater wound on the side of a swordfish caught in the Gulf of Mexico. (Photo by Martin Bartlett.)

Thunnus albacares (Bonnaterre); dolphin, *Coryphaena hippurus* Linnaeus; opah, *Lampris regius* (Bonnaterre); and swordfish, *Xiphias gladius* (Linnaeus) (Figure 2). In addition to these, I have seen crater wounds on albacore, *Thunnus alalunga* (Bonnaterre), and wahoo, *Acanthocybium solandri* (Cuvier), in the central Pacific. Biologists and fishermen in Hawaii have reported to me having seen them on kawakawa, *Euthynnus affinis* (Cantor); large jacks, *Caranx* sp.; rainbow runners, *Elagatis* sp.; and various species of marlins, *Istiophoridae*.

The cetaceans upon which crater wounds, crescentic wounds, or resultant scars have been reported were listed by van Utrecht (1959). Included were beaked whales, sperm whales, various species of porpoises, and nearly all of the baleen whales (order Mysticeti) except the right whales (family Balenidae) which apparently do not migrate out of cold polar waters. In Hawaiian waters, wounds and scars (Figure 3) are commonly seen on porpoises of the genera *Tursiops* and *Stenella*, and have been observed on a beaked whale, *Ziphias* sp., stranded on Oahu.

Dr. Donald W. Strasburg, during discussions several years ago, planted the idea that *Isistius* might be the cause of crater wounds on fishes. He had found (Strasburg, 1963) that the man-

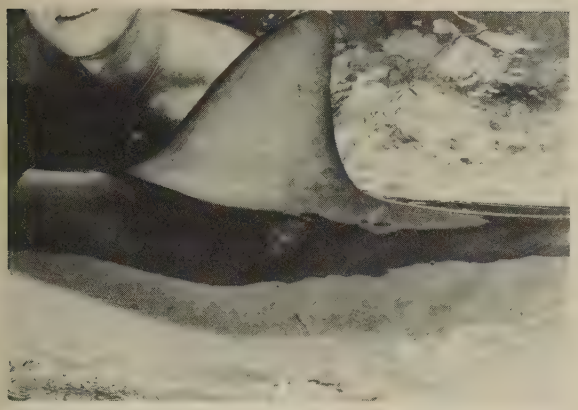

FIGURE 3.—Crescentic scar on a living porpoise, *Stenella roseiventris* Wagner, The Oceanic Institute, Makapuu, Hawaii.

dibular teeth of *Isistius* are shed as a unit and that the next set of replacement teeth are already erect and immediately functional when the previous set is shed. He wondered " . . . which aspects of *Isistius* biology require such a safeguard."

OBSERVATIONS

An opportunity to test the idea came in July 1969, during cruise 44 of the RV *Townsend Cromwell* of the NMFS, HAFRC (National Marine Fisheries Service, Hawaii Area Fishery Research Center). Nightly midwater trawl hauls were made along long 145° W between lat 14° N and 3° S in the central Pacific. The trawl catches contained occasional specimens of *Isistius*, some of which were alive but moribund when brought on board. I stated that this species of shark might be responsible for the crater wounds which we had observed on tunas a few hours earlier. This led John D. Fowler, Jr., research assistant aboard the *Townsend Cromwell*, to press the mouth of a moribund *Isistius* against the side of a dead fish, *Cubiceps* sp. The shark made a biting motion, producing a crescentic wound (Figure 4) that if completed would have been similar in size and shape to crater wounds observed on tunas. That shark could not be induced to repeat its performance, but Fowler's experiment led to further attempts to determine

FIGURE 4.—A crater "wound" produced on the surface of a nectarine by pushing the teeth of a dead *Isistius* into the fruit and then rotating the body of the shark around the point of attachment. In the center is a crescentic "wound" produced by a living *Isistius* when its mouth was pressed against the side of the dead fish.

whether adaptations in structure for specialized feeding behavior existed in *Isistius*.

The basihyoid cartilage or "tongue" of *Isistius* was large and thick in contrast to that structure in galeoid sharks. It was also unusually movable; with a pencil I was able to push the tongue caudad to a point just anterior to the first exterior gill opening (Figure 5). In that position the posterior margin of the tongue was elevated (dorsad) until the tongue was nearly vertical, fitting closely against the roof of the mouth, and

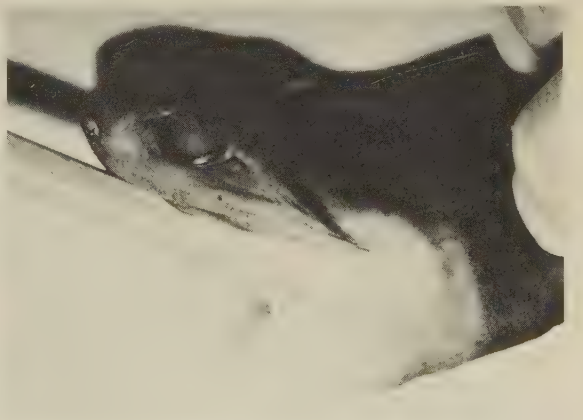

FIGURE 5.—A demonstration of the movability of the tongue of *Isistius*.

completely separating the mouth from the pharynx. Two ridges in the roof of the mouth corresponded to two grooves in the posterior margin of the tongue. This structural correspondence suggested that vertical positioning of the tongue was a normal occurrence. The movability of the tongue, as well as several other attributes described below, can only be demonstrated with specimens of *Isistius* that have not been fixed.

Observations of these anatomical characters led to the hypothesis that *Isistius* is capable of achieving a vacuum with its mouth on a smooth surface. Concurrently with the retracted, vertical positioning of the tongue, the lips protruded completely around the mouth. The fleshy lateral lips contained well-developed labial cartilages that caused them to be semirigid and, when protruded, to complete an ovoid of labial margins in a single plane (Figure 6). Such a structure in contact with a smooth surface enables the

FIGURE 6.—A demonstration of the coracohyoideus muscles of *Isistius*. Note also the protruded lips, the internal openings of the spiracles, and the mandibular teeth.

shark to form a vacuum when the spiracles are closed and the tongue then retracted.

In order to further determine if behavioral retraction of the tongue was probable, dissections were made of the ventral surface of the shark just posterior to the mandible. The paired coracohyoideus muscles that insert on the tongue were unusually large in *Isistius* (Figure

FIGURE 7.—Exposed coracohyoideus muscles of a large whitetip shark, central Pacific.

6). A comparative dissection of a large, fresh, whitetip shark, *Carcharhinus longimanus* (Poey) was made (Figure 7); the cross sectional areas in *Isistius* were estimated to be four times those of the same muscles in the whitetip shark, both relative to the total lengths of the sharks. Pulling caudad on the exposed coracohyoideus muscles of *Isistius* caused the tongue to retract to the nearly vertical position noted before; concurrently, the mouth gaped and the lips protruded. The tongue of the whitetip shark was not movable and pulling on the coracohyoideus muscles did not retract it.

Later I attempted to repeat Fowler's experiment by holding the mouth of a living *Isistius* against the side of a gempylid fish. In this case, the shark did not make a biting motion but, instead, the spiracles closed, the head flattened slightly, and an oral vacuum was formed by means of which I was able to lift the gempylid from the table with no other support.

It seemed that the remaining evidence needed to indict *Isistius* would be the presence of hemispheroidal plugs of fish flesh in their stomach contents. This evidence was found when two *Isistius* caught subsequently on the same cruise were found to contain single plugs of flesh of appropriate size and shape. One of these plugs was from a relatively large fish, judging from the thickness of the myomeres; the other was from a squid. During a later cruise in the same area, Reginald M. Gooding, fishery biologist,

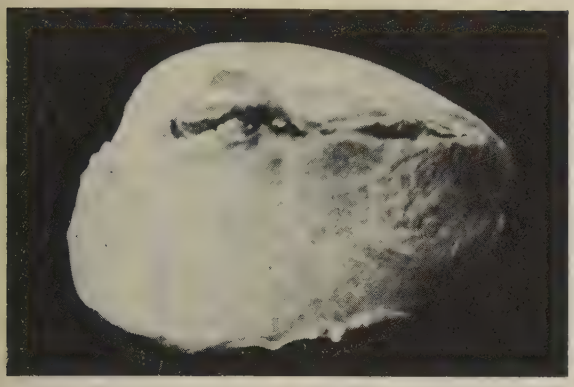

FIGURE 8.—A hemispheroidal plug of unidentified fish flesh from the stomach of an *Isistius*, central Pacific.

found a very fresh plug of fish flesh complete with integument and some scales (Figure 8). The fishes from which these plugs were bitten have not been identified. In order to find such plugs, it is necessary to examine *Isistius* immediately after capture because digestion will usually continue for a time after the specimen is placed in formaldehyde or a freezer.

DISCUSSION

Further evidence relating *Isistius* to wounds on fishes may be present in a photograph (Figure 9) of a crescentic wound on the caudal fin of a swordfish (M. R. Bartlett, personal communication). The deep crescentic cut is opposed by an arc of small dents and scars. The size and arrangement of these correspond to the small, hooked upper teeth of *Isistius* (Figure 6). In addition, a series of white scratches extending from the small arc toward the crescentic cut appear to have been made by the upper teeth as the shark backed away from the incomplete bite. In this case, the shark's mandibular teeth must have encountered the large, bony ray in the edge of the caudal fin. The same fin bore an entire, cut-out wound near the posterior border (Figure 10).

The geographical distribution of records of *Isistius brasiliensis* (Strasburg, 1963; Parin, 1964) corresponds well with the general distributions of the species of fishes which bear crater wounds. Several authors (Mackintosh and

FIGURE 9.—A crescentic wound on the caudal fin of a swordfish caught in the Gulf of Mexico. Note the arc of small dents opposite the cut, and the scratches produced by the shark's upper teeth as it backed away from the incomplete wound. (Photo by Martin Bartlett.)

Wheeler, 1929; Pike, 1951; Nemoto, 1955; van Utrecht, 1959) have noted that fresh wounds were seen only, or more frequently, on cetaceans caught in the warmer waters of their migrations and that those caught more poleward bore only healed or partially healed scars. This was evidence, they stated, that the animal producing the wounds was an inhabitant of warm water.

Some wounds on cetaceans described in the literature were undoubtedly produced by lampreys (Pike, 1951). The majority of catch records of lampreys in both the Pacific and Atlantic, however, are near shore and in temperate or cold waters which fits poorly the distribution of fishes and whales bearing fresh crater wounds.

The largest crater wounds recorded (Mackintosh and Wheeler, 1929) were 4 or 5 cm by 7 cm. The smallest I have seen were 1.2 cm by 2 cm. The smaller diameters of these correspond well with the bite-widths I have estimated for *Isistius* at the extremes of the known range of 14 to 50 cm, total lengths (Strasburg, 1963).

All of the *Isistius* stomachs examined aboard the *Townsend Cromwell* contained squid beaks and pieces of squid pens. Strasburg (1963) also

FIGURE 10.—The caudal fin of a swordfish caught in the Gulf of Mexico, showing a crescentic wound and a completed wound cut through the trailing edge of the fin.

found squid remains in most of the stomachs of preserved specimens he inspected, and calculated that the squids which were eaten were as large or larger than the sharks. He wondered how small sharks that apparently swim slowly could catch and capture such large, swift prey.

This question is also pertinent in considering how *Isistius* succeeds in contacting fast-swimming animals such as tunas, marlins, or porpoises. It would appear to be no problem for *Isistius* to approach and make contact with basking or drifting whales or fishes. In the case of tunas, however, there is no evidence that they ever drift or stop swimming (Magnuson, 1970). A possible sequence is that the potential prey, seeing *Isistius* as an object apparently suitable for food, makes the initial approach, identifies it at a short distance, rejects it as food, and veers off. At that instant, the shark may be able to achieve contact by means of a short dash.

It is also possible that the shark, to some degree, simulates other organisms such as squids in the pattern of its luminous ventral surface. A more remote possibility is that *Isistius* is mistaken by large teleosts for a cleaner, and is invited to make contact.

Large squids appear to be killed by *Isistius* more often than merely deprived of plugs of flesh. It may be that squids also make an initial approach but, unlike teleosts, do not veer off from their attack and are subsequently bested in the encounter.

Isouchi (1970) provided the only record of an *Isistius* eaten by a large teleost when he found a living shark in the stomach of *Scomberomorus* sp. This record indicates that *Isistius* is a potential food item; on the other hand, records of teleosts having ingested any species of small or young sharks are limited to five or six (S. Springer and M. R. Bartlett, personal communications). This certainly supports a hypothesis of usual rejection. Rejection of the young as food by teleosts, in fact, may account for the survival of most elasmobranch species, considering their extremely low reproduction rates and relatively low swimming speeds.

It may not be necessary to assume any complicated behavior patterns of *Isistius* or its prey; perhaps contacts by means of short dashes can be made during chance proximities. Thomas Dohl, The Oceanic Institute, Hawaii, has informed me that young porpoises of sizes that are assumed to be still nursing do not bear wounds or scars, but those which are larger do. Similar restriction of wounds and scars to older porpoises is suggested by the data of van Utrecht (1959). This may be simply a matter of an increased probability of encounter with time; but it may, on the other hand, indicate that porpoises are not attacked by *Isistius* until the porpoises become predatory on fish.

Several crescentic wounds which I have examined on tunas were made from a frontal attack

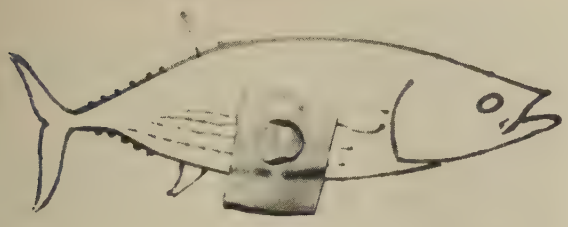

FIGURE 11.—An excised crescentic wound superimposed over a diagram of a skipjack tuna to indicate that the wound was made from a frontal attack, central Pacific.

position, that is, the shark and its prey were going in opposite directions when the wound was inflicted (Figure 11). Such crescentic wounds, as previously pointed out, are apparently the result of circumstances which do not allow the shark to complete the scooping out process. Besides providing support for the suggestion that the teleost makes the initial approach, the evidence of frontal attacks may explain the occurrence of wounds in which the plug of flesh is still attached to the bottom of the wound by a peduncle. Such wounds are common on cetaceans (Mackintosh and Wheeler, 1929; van Utrecht, 1959). In a frontal attack, the drag of water on the shark's body would cause it to rotate, in the manner of the hand of a clock, around the point of attachment until the shark was oriented in the same direction as its prey. This movement would cause the mandibular teeth to act in the manner of a melon-ball cutter and, if penetration was adequate, the crater wound would be completed.

To explore this possibility, I employed a nectarine (*Persicum* sp.) from the ship's galley since no large, dead fish was available at the moment. I pushed the teeth of a fresh, dead *Isistius* into the fruit and then rotated the body around that point. The result (Figure 4) was a neat, round, crater "wound" and the hemispheroidal "plug" in the shark's mouth with the small, hooked upper teeth securing it. If tooth penetration had been inadequate during such a sequence, the integument would be cut completely around but the plug would remain attached by a central peduncle. Necrosis of the plug would probably follow, resulting in conditions described by Mackintosh and Wheeler (1929). They presented a hypothetical sequence beginning with a crescentic wound which developed, by gradual erosion of the flesh, to the open pit stage. The "flabby" pedunculate plug, they believed, was a stage in the healing process and was sloughed off near the completion of healing.

They pointed out that the most obvious cause of crescentic and open pit wounds was the bite of some fish, but no fish known to them possessed teeth or a mouth structure which would produce such wounds. They, therefore, returned to the assumption that the wounds were a result of microbial infections.

Except in the cases of attacks on squids when the prey is killed, it appears that *Isistius*, in biting pieces out of living cetaceans and fishes, qualifies as a temporary parasite in the same sense that a mosquito does.

ACKNOWLEDGMENTS

I want to acknowledge the contributions of many persons who provided unpublished records, specimens of wounds and scars, photographs, as well as ideas and encouragement during the preparation of this manuscript. My special thanks are extended to John D. Fowler, Jr., NMFS, HAFRC, who initiated the important experiments at sea.

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THE RELATIVE IMPORTANCE OF NANNOPLANKTON AND NETPLANKTON AS PRIMARY PRODUCERS IN THE CALIFORNIA CURRENT SYSTEM

THOMAS C. MALONE[1]

ABSTRACT

Nannoplankton and netplankton primary productivity and standing crop were measured on a seasonal basis in Monterey Bay (October 1969 to February 1971) and along four transects of the California Current between lat 35° and 50° N. Nannoplankters accounted for 60 to 99% (mean = 86%) of the observed productivity and standing crop both inshore and offshore under oceanic conditions. Seasonal and geographical variations in the nannoplankton fraction were remarkably stable, and variations in phytoplankton productivity and standing crop were due primarily to the netplankton. The assimilations ratios of both fractions were relatively constant.

Increases in the netplankton fraction were closely coupled with the occurrence of coastal upwelling, and netplankton productivity and standing crop exceeded that of the nannoplankton only during the strongest upwelling pulses. These increases were probably due to the suspension effect of positive vertical advection and to increases in ambient NO_3-N concentrations above 1 to 3 μM. Decreases were in response to increases in grazing pressure and downward water movements. A model is suggested to account for the following observations: (1) the nannoplankton fraction varied within narrow limits compared with the netplankton; (2) nannoplankton assimilation ratios (and presumably growth rates) were consistently high and twice those of the netplankton; and (3) netplankton productivity and standing crop increased relative to the nannoplankton during periods of upwelling. The model is based on the response of particles of varying sinking rates to vertical and horizontal advection, and on the degree of coupling between the production of organic matter by primary producers and grazing by primary consumers.

The phytoplankton can be divided into two size classes based on their retention by fine mesh nets (aperture size 20 to 90 μ). Those retained are commonly called "netplankton" while those which escape are referred to as "nannoplankton." Seasonal and geographic variations in netplankton and nannoplankton primary productivity and standing crop are neither well documented nor understood. Previous investigations in both temperate (Yentsch and Ryther, 1959; McAllister et al., 1959; Gilmartin, 1964; Anderson, 1965) and tropical marine environments (Steeman Nielsen and Jensen, 1957; Holmes, 1958a; Teixeira, 1963; Saijo and Takesue, 1965; Malone, in press a) have demonstrated that the nannoplankton are usually responsible for 80 to 100% of the observed phytoplankton productivity and standing crop. Netplankton productivity is often higher in neritic than in oceanic waters (e.g., Steeman Nielsen and Jensen, 1957; Malone, in press a) but rarely exceeds that of the nannoplankton. However, neritic phytoplankton communities dominated by the netplankton in terms of cell number (Digby, 1953) and chlorophyll concentration (Subrahmanyan and Sarma, 1965) have been reported.

The ecological significance of these two size classes lies in the role of cell size and surface area-to-volume (A/V) ratios in the dynamics of phytoplankton productivity and energy flow through pelagic food chains. Small cells generally have shorter generation times and higher growth rates in a given environment than do larger cells (Findenegg, 1965; Williams, 1965; Eppley and Sloan, 1966; Eppley and Thomas, 1969; Eppley et al., 1969). Recent observations on the kinetics of nutrient uptake by phytoplankton (Eppley et al., 1969) indicate that the half-saturation constants (K_s) for nitrate and ammo-

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nium uptake vary in proportion to cell size, presumably a consequence of the high A/V ratios of smaller cells (Munk and Riley, 1952). Some evidence is also available that maximum uptake rates (V_m), while not species specific, do increase with increasing cell size (Dugdale, 1967; Eppley et al., 1969) so that netplankters with high K_s and V_m values would be favored when nitrate concentrations are high while nannoplankters with low K_s and V_m values would be favored when nitrate concentrations are low.

High A/V ratios facilitate suspension (Munk and Riley, 1952; Smayda and Boleyn, 1966a, b; Eppley et al., 1967) increasing the potential residence times of cells in the photic zone under stratified conditions. Also, since sinking rates generally increase as cell size increases, larger cells will tend to be concentrated in regions of upward water flow while smaller cells will be distributed along a gradient toward regions of downward water flow (Stommel, 1949; Semina, 1968). In this way, small cells will tend to be spread over a greater volume than larger cells, and motile cells seeking to maintain their position in the water column will be concentrated in regions of downward flow (Hutchinson, 1967).

In addition, the distribution of productivity and biomass among different size classes of phytoplankton should be reflected in the distributions and abundances of herbivores which selectively graze on the basis of particle size. Nannoplankters appear to be the preferred food of many planktotrophic larvae (Bruce et al., 1940; Thorson, 1950) and microzooplankton (Beers and Stewart, 1969; Parsons and Le Brasseur, 1970), while herbivorous copepods actively select netplankton species (Harvey, 1937; Mullin, 1963; Conover, 1966; Mullin and Brooks, 1967; Richman and Rogers, 1969). Phytoplankton cell size may also affect the efficiency of energy transfer to large predators, since nannoplankton-based food chains appear to require one or two additional energy transfers to reach a given sized consumer than do netplankton-based food chains (Ryther, 1969; Parsons and Le Brasseur, 1970).

The California Current system and Monterey Bay provide ideal environments in which to study variations in netplankton and nannoplankton productivity and standing crop, since nutrient concentrations and vertical water movements vary markedly both seasonally and geographically. The California Current system is discussed by Reid et al. (1958), and the monthly mean charts of geostrophic flow have been prepared by Wyllie (1966). The southerly flow of the California Current is typically strongest during the spring and summer when northerly winds are best developed. At this time the coastal boundary of the Current is marked by upwelling. During the fall and winter northerly winds are weak or reversed, and a coastal countercurrent (the Davidson Current) often develops between the California Current proper and the coast. Thus, the hydrography of the coastal region off California is generally characterized by upward water movements and high nutrient concentrations during the spring and summer, and downward water movements and low nutrient concentrations during the fall and winter.

The annual cycle of hydrographic conditions in Monterey Bay has been described by Bolin and Abbott (1961) and Bolin (1964). Skogsberg (1936) divided the annual cycle in the upper 100 m into three hydrographic periods:

1. An Upwelling Period (March to September) characterized by low surface temperatures (9.5° to 11.5° C), high salinities (33.2 to 33.9‰), and high nutrient concentrations (>2.0 μM PO_4-P, >5.0 μM NO_3-N, and >10.0 μM SiO_3-Si).
2. An Oceanic Period (September to November) characterized by high surface temperatures (12.0° to 15.0° C), decreasing salinities (33.0 to 33.6‰) and low nutrient concentrations (0.2 to 2.0 μM PO_4-P, 0.0 to 0.5 μM NO_3-N, and 1.0 to 10.0 μM SiO_3-Si).
3. The Davidson Current Period (November to March) characterized by decreasing temperatures (11.0° to 13.5° C), low salinities (32.4 to 33.2‰), and low nutrient conditions.

Water of oceanic origin is brought into the Bay during both Oceanic and Davidson Current Periods, at first passively as the high density upwelled water begins to subside and then actively

when southerly winds prevail. Since both periods are characterized by a downward flux of water (subsidence and downwelling) and low nutrient concentrations in the upper half of the photic zone, they will be consolidated and referred to as the "Oceanic Period."

The purpose of this study is to document temporal and spatial variations in nannoplankton and netplankton productivity and standing crop and to evaluate these variations with respect to dissolved inorganic nitrogen concentrations, vertical water movements, and grazing pressure.

METHODS AND MATERIALS

Measurements of netplankton and nannoplankton primary productivity and standing crop were made at 17 stations in the California Current system between lat 35° and 50° N during July, August, and November 1970, and at California Cooperative Oceanic Fisheries Investigations (CalCOFI) station 3 in Monterey Bay from October 1969 to February 1971 (Figure 1). The latter station is located over the Monterey Submarine Canyon in about 1000 m of water (lat 36°46.8′ N, long 122°01′ W). All data were collected during cruises of the RV *Proteus* (Stanford University).

Netplankton and nannoplankton photosynthetic capacities (rate of carbon fixation as measured by the carbon-14 technique at light saturation), chlorophyll-a concentrations, and cell numbers were estimated from duplicate water samples collected from 2 m below the surface with two Van Dorn bottles. The duplicate Van Dorn bottle samples were taken 3 hr before local apparent noon and again 3 hr after local noon. Four light and two dark bottles (a total of 12 125-ml Pyrex bottles) were drawn from each sample, inoculated with 5 μc of $Na_2{}^{14}CO_3$, and incubated under fluorescent light (about 0.06 langley/min) for 2 to 3 hr at sea-surface temperatures (Doty and Oguri, 1958). Following incubation, half of the light and dark bottles from each Van Dorn sample were fractionated by passing the water first through Nytex-net discs with 22-μ apertures (netplankton) and then through HA Millipore[2] filters (nannoplankton). The remaining four light and two dark bottles were HA Millipore filtered directly as controls. The filter discs were washed with about 30 ml of filtered seawater, dried in a CO_2 free atmosphere, and their activity measured with a Nuclear Chicago scalar (model 161A) equipped with a model D47 gas flow chamber with a micromil window. Each filter was counted for at least 5 min, and rates of carbon fixation were calculated as described by Doty and Oguri (1958) after averaging duplicate light bottle values. Mean coefficients of variation between duplicate light bottles were 6 ± 1% for the nannoplankton and 26 ± 5% (95% confidence limits) for the netplankton. The mean coefficient of variation between phytoplankton productivity values calculated from the sum of the nannoplankton and netplankton fractions and the unfractioned controls was 10 ± 2%.

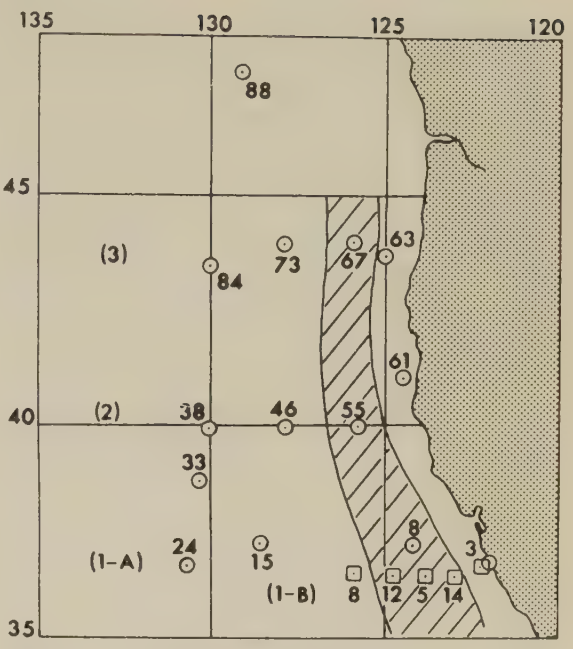


FIGURE 1.—Stations occupied along transects (1-A, B, 2, and 3) of the California Current during July and August (⊙) and during November (□), 1970; the shaded area represents the transition zone between offshore and inshore regions.

[2] The use of trade names is merely to facilitate descriptions; no endorsement is implied.

Samples for pigment analysis were also collected 2 to 3 hr before local apparent noon from 13 depths between the surface and 100 to 200 m. The upper 6 to 10 depths sampled were within the photic zone, depending on its depth, and were chosen on the basis of the thermal structure of the water column. Sample depths were evenly spaced through the mixed layer and evenly but more closely spaced across the thermocline. Samples were always taken at the base of the photic zone and at two depths below to at least twice the photic zone depth. Chlorophyll-a and phaeopigment concentrations were determined by a fluorometric technique (Strickland and Parsons, 1968). Water samples were fractionated by the same procedure described for the carbon-uptake experiments except Whatman GF/C glass fibre filters coated with 2 ml of 1% $MgCO_3$ suspension were used in place of membrane filters, and the netplankton chlorophyll fraction was calculated from the difference between fractionated and unfractionated values. Duplicate values for each fraction were averaged (mean coefficients of variation were 10 ± 2% for the nannoplankton and 22 ± 8% for the netplankton fraction). The use of glass filters may have led to no more than a 10% underestimation of nannoplankton chlorophyll-a (Malone, in press a).

Samples for phytoplankton enumeration and identification were preserved with Lugol's solution made basic with sodium acetate in place of acetic acid. Aliquots of 100 ml were placed in Nessler tubes and the cells allowed to settle for 72 hr. Depending on the concentration of cells, from 50 to 90 ml of the supernatant was then siphoned off and 2 ml aliquots were added to settling chambers. After 48 hr the samples were counted by the inverted microscope technique of Utermöhl (Lund et al., 1958). All organisms longer than about 30 μ were counted at 100× while smaller cells were counted in 100 random fields at a magnification of 400×. For lack of better criteria, phytoplankton having dimensions of 30 × 22 μ or less were classified as nannoplankton and those with larger dimensions as netplankton. This did not present much of a problem, however, because the nannoplankton fraction was dominated by cells whose longest dimension was in the range of 2 to 15 μ, while the netplankton fraction was dominated by chain-forming diatoms with cell lengths of 40 μ or more, e.g., *Nitzschia pacifica*. Dominant netplankton forms were identified to species, and less numerous forms to genus. The remaining phytoplankters were classified as pennate or centric diatoms, thecate or nonthecate dinoflagellates, coccolithophores, silicoflagellates, or "others." Mean coefficients of variation between duplicate samples were 14 ± 4% for the nannoplankton fraction and 27 ± 11% for the netplankton fraction.

Standard hydrographic and bathythermograph casts were made 2 to 4 hr before local apparent noon in conjunction with productivity and standing crop measurements to estimate the vertical distributions of dissolved inorganic nitrogen compounds, temperature, and density in the water column. Additional hydrographic casts made for the CalCOFI Program in Monterey Bay are utilized in this paper. Nitrate concentrations were determined by the manual procedure described by Strickland and Parsons (1968) and ammonium by the phenolhypochlorite method (Solorzano, 1969). A Secchi disc was used to estimate photic zone depths (3.5 × Secchi disc reading).

The ratio of phaeopigments-to-chlorophyll in the water column (to 100 m for inshore stations and to 200 m for offshore stations) was used as a rough index of relative grazing pressure on the phytoplankton standing crop (Lorenzen, 1967; Beers and Stewart, 1969). In the present study, a highly significant ($P = 0.01$) regression of phaeopigment concentration on $\log_{10}$ transformed zooplankton wet weights was found, and it was concluded that the phaeopigment-chlorophyll ratio could be used as a first order index of grazing pressure.

TEMPORAL VARIATIONS IN MONTEREY BAY

ENVIRONMENTAL FACTORS

The hydrographic conditions observed at CalCOFI 3 from October 1969 to February 1971 are summarized in Figure 2 and Table 1. Sur-

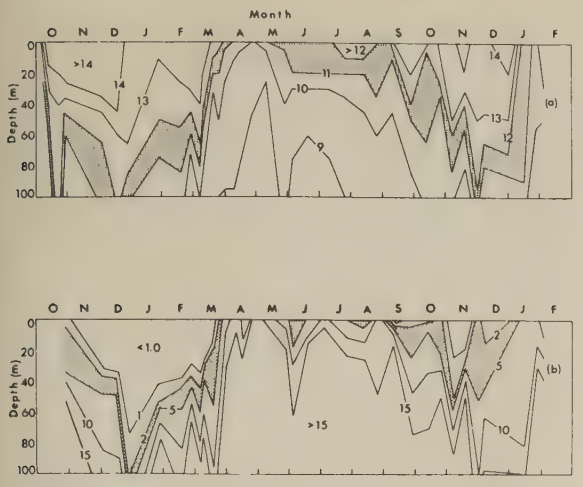


FIGURE 2.—a. Vertical distribution of temperature (°C) at CalCOFI 3 from October 1969 to February 1971. b. Vertical distribution of NO_3-N (μM).

TABLE 1.—Environmental factors monitored at the surface, concurrently with measurements of productivity and standing crop at CalCOFI station 3 in Monterey Bay.

Date	Temperature	Salinity	NO_3-N	NH_4-N	Mixed layer	Photic zone
	°C	‰	μM	μM	m	m
28 Oct. 69	14.20	33.51	1.7	--	30	60
2 Dec.	14.68	33.39	0.3	--	30	55
26 Feb. 70	13.10	32.68	0.3	0.3	50	60
5 Mar.	13.20	32.99	0.4	0.6	30	50
10 Mar.	13.17	32.98	0.1	0.2	25	65
18 Mar.	12.06	33.11	0.4	0.4	15	30
31 Mar.	11.17	33.49	7.8	0.3	0	25
8 Apr.	10.45	33.65	14.5	0.1	30	45
18 June	12.44	33.81	6.5	0.5	10	15
2 July	11.02	33.71	13.9	1.5	0	40
26 July	12.95	33.82	6.5	3.3	0	40
12 Oct.	13.56	33.53	1.1	0.6	0	70
26 Oct.	13.03	33.41	3.1	0.8	30	65
6 Nov.	13.59	32.99	0.7	0.2	40	65
18 Nov.	14.29	33.26	0.2	--	15	60
30 Nov.	13.40	33.28	2.4	--	45	55
7 Dec .	13.24	33.02	1.3	--	50	55
17 Jan. 71	11.50	33.43	6.6	0.4	50	60
27 Jan.	10.84	33.52	8.7	0.8	20	30
3 Feb.	11.79	33.33	3.8	0.4	15	50

face water of oceanic origin was found in the Bay from October 1969 to mid-March 1970. The intrusion of oceanic water and the general subsidence of the water mass are evidenced by the descending isotherms and nitrate isopleths, high surface temperatures, and low salinities. Mixed layer and photic zone depths were about 30 and 60 m respectively, and NO_3-N concentrations were less than 0.5 μM throughout most of the photic zone.

Upwelling was initiated in March as indicated by the ascending isotherms and nitrate isopleths, NO_3-N concentrations in excess of 5.0 μM over the entire photic zone, low surface temperatures, and high surface salinities. With the exception of a minor intrusion of oceanic water late in July and early August, upwelling continued uninterrupted into September with peaks in early April and early September. "Mixed layer" depths varied between 0 and 30 m, and at no time exceeded the depth of the photic zone, which ranged from 15 to 45 m.

From September through December the hydrography of the Bay was confused and neither oceanic nor upwelling conditions ever predominated. Weak upwelling surges bracketed by influxes of oceanic water occurred during late October and late November (Figure 2). Surface NO_3-N concentrations were variable (0.2 to 3.1 μM) reflecting the indecisiveness of the system. Then, following a period of oceanic water during December and early January, a strong upwelling pulse occurred which was about as intense as the upwelling during late March and early April of the previous year.

Hydrographically, three periods can be distinguished in the Bay during the period of this study:

1. A stable Oceanic Period from October 1969, into March 1970,
2. A stable Upwelling Period from March into September,
3. A "Mixed" Period from September through December punctuated by a strong upwelling pulse in January.

The grazing pressure index declined during the transition from oceanic to upwelling conditions to a low of 0.03 in early April (Figure 3). Grazing pressure then increased rapidly during the steady upwelling of June and July to an annual maximum of 2.03 which was followed by a gradual decline during the Mixed Period ending with a sharp rise in late January to a peak in early February.

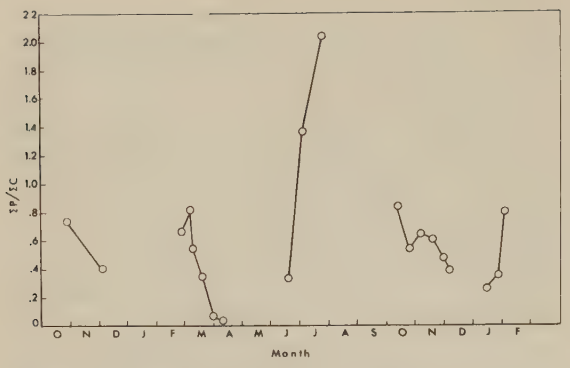


FIGURE 3.—Temporal variations in the ratio of phaeopigments-to-chlorophyll-a (P/C) integrated over the upper 100 m at CalCOFI 3.

SURFACE PRIMARY PRODUCTIVITY AND STANDING CROP

Seasonal variations in surface productivity and standing crop are shown in Figure 4. Since a significant difference (F-test, $P<0.01$) was not observed between morning and afternoon values (see Malone, in press b), only data collected during the morning sampling will be considered.

Phytoplankton productivity and standing crop remained below 5.0 mgC m^{-3} hr^{-1}, 1.00 mgChl-a m^{-3}, and 3.5 $\times$ 10^5 cells/liter during the Oceanic Period. Values above 10.0, 1.50, and 10.0 $\times$ 10^5 were observed only during the Upwelling Period and the January Upwelling pulse. The Mixed Period was characterized by intermediate levels of productivity and standing crop. Three peaks were observed, of which the two greatest coincided with the two most intense upwelling pulses: (1) 50.4 mgC m^{-3} hr^{-1}, 7.92 mgChl-a m^{-3}, and 24.2 $\times$ 10^5 cells/liter on the last day of March, and (2) 43.4, 10.46, and 23.9 $\times$ 10^5 during the last week of January. The third, less pronounced peak, was in mid-June during steady upwelling.

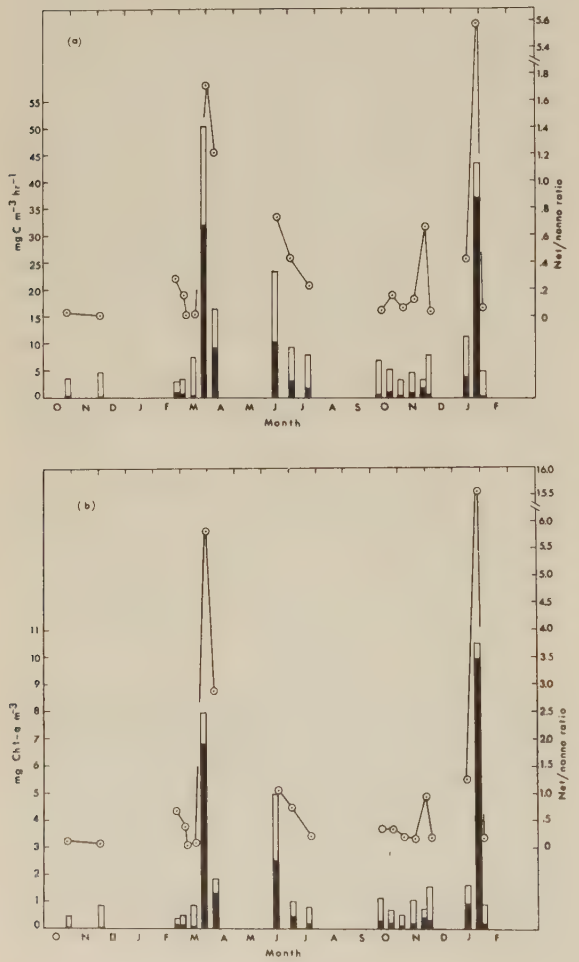
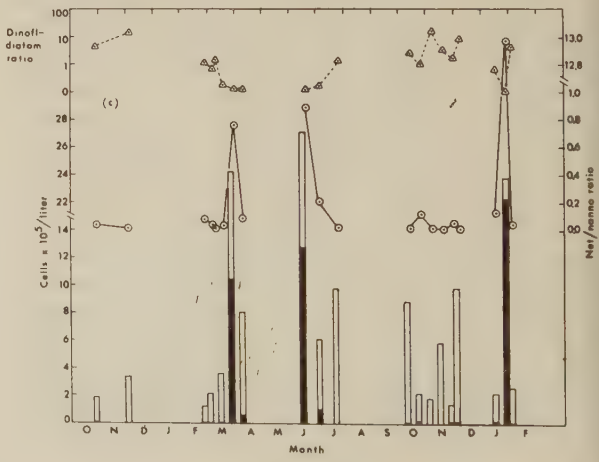


FIGURE 4.—a. Temporal variations in surface netplankton (■) and nannoplankton (□) productivity (mgC m^{-3} hr^{-1}) and the net/nanno ratio (⊙) at CalCOFI 3. b. Temporal variations in surface chlorophyll-a (mg m^{-3}) and the net/nanno ratio. c. Temporal variations in surface cell numbers, the net/nanno ratio, and the ratio of dinoflagellates-to-diatoms (△).



Phytoplankton assimilation ratios (mgC hr^{-1} mgChl-a^{-1}) were relatively constant, with most values falling between 5 and 10 (mean = 7.4 ± 1.0, 95% confidence limits). Fluctuations in the amount of chlorophyll-a per cell (10^{-6} μg) were also within comparatively narrow limits. Values varied from 0.85 to 6.97 with a mean of 2.62 ± 0.66.

Surface levels of nannoplankton productivity and standing crop were remarkably stable through the year. Productivity and standing crop values were less than 8.0 mgC m^{-3} hr^{-1}, 0.80 mgChl-a m^{-3}, and 3.3 × 10^5 cells/liter during the Oceanic Period. During the Upwelling Period productivity ranged from 6.6 to 18.6, chlorophyll-a from 0.46 to 2.44, and cell numbers from 5.1 to 14.4 × 10^5. Thus, while nannoplankton productivity and standing crop were lower under oceanic than upwelling conditions, the differences were not marked.

In contrast, netplankton productivity and standing crop varied tremendously during the year, from less than 0.6 mgC m^{-3} hr^{-1}, 0.14 mgChl-a m^{-3}, and 0.1 × 10^5 cells/liter during the Oceanic Period to greater than 2.8, 0.40, and 0.6 × 10^5 during the Upwelling Period. Two prominent peaks were observed (31.8 mgC m^{-3} hr^{-1}, 6.76 mgChl-a m^{-3} and 36.8 and 9.83), both in association with the two most intense upwelling pulses. A secondary peak occurred in mid-June. Netplankton cell numbers reached successive peaks of 24.2, 27.1, and 23.8 × 10^5 cells/liter which coincided with peaks in productivity and chlorophyll-a. During the fall and early winter Mixed Period, intermediate values were observed with small peaks associated with each short burst of upwelling. Thus, netplankton productivity and standing crop varied from an order of magnitude less than that of the nannoplankton during the Oceanic Period to an order of magnitude greater during the Upwelling Period. Comparison of mean squares and ranges of variation (Table 2) clearly demonstrates that temporal variations in phytoplankton productivity and standing crop were primarily due to the netplankton fraction with the nannoplankton maintaining a relatively stable background level.

Variations in the ratio of netplankton-to-nannoplankton (net/nanno) are also shown in Figure 4. The net/nanno productivity ratio never exceeded 0.3 during intrusions of oceanic water (either during the Oceanic Period or the Mixed Period), and was greater than 1.0 on only two occasions: during the strong upwelling pulses of late March and late January. The same pattern was found for the net/nanno chlorophyll and cell number ratios except the chlorophyll ratios were consistently higher and the cell number ratios lower than the productivity ratios. This is reflected in the assimilation ratios and cell chlorophyll-a content of the two fractions, both of which were relatively constant during the study. The mean nannoplankton assimilation ratio of 9.4 ± 1.5 was significantly higher than the netplankton mean of 4.7 ± 1.3. Similarly, the nannoplankton had more cells per unit chlorophyll-a than did the netplankton. The mean chlorophyll-a content per netplankton cell was 23.6 ± 13.1 × 10^{-6} μg which is significantly higher than the nannoplankton mean of 1.9 ± 0.5 × 10^{-6} μg.

Peaks in the ratio of netplankton-to-nannoplankton cell numbers coincided with peaks in netplankton cell number, but the ratio exceeded 1.0 only during the January bloom. This probably reflects the dominance of the small-celled (<20 μ in length), chain-forming diatoms *Chaetoceros socialis* and *Skeletonema costatum* in the netplankton fraction. In contrast, the netplankton blooms of late March and mid-June were dominated by large-celled (>40 μ in length) chain-forming diatoms *Nitzschia pacifica* and *Rhizosolenia fragilissima*, respectively. *Nitzschia* spp., *Skeletonema costatum*, *Leptocylindricus* sp., and *Chaetoceros* spp. accounted for

TABLE 2.—Mean squares and range factors (maximum/minimum) for nannoplankton and netplankton productivity (PP = mgC m^{-3} hr^{-1}), chlorophyll-a concentration (mg m^{-3}, m^{-2}), and cell numbers (no./liter) at CalCOFI station 3.

Fraction	Mean squares			
	PP	*mg* m^{-3}	*no./liter*	*mg* m^{-2}
nannoplankton	16	0.2	17	86
netplankton	109	6.5	32	1,680
	Range factors			
nannoplankton	9	12	13	4
netplankton	1,800	4,200	4,400	120

70% of the netplankton in the March bloom. In mid-June *Rhizosolenia* spp. and *Nitzschia* spp. made up 80% of the netplankton. The nannoplankton fraction was dominated by small monads 2 to 15 μ in length in all but one of the samples examined. The one exception occurred at the peak of the March-April netplankton bloom when small diatoms dominated the nannoplankton fraction. When the net/nanno ratio was high (during upwelling), diatoms were more numerous than dinoflagellates; but when the ratio was low (during oceanic conditions), dinoflagellates were more numerous (Figure 4c).

VERTICAL DISTRIBUTION OF PIGMENTS

The chlorophyll-a content of the water column (0 to 100 m) varied between 14 and 30 mg m^{-2} during the Oceanic Period and between 24 and 152 mg m^{-2} during the Upwelling Period (Figure 5). The seasonal pattern of variation was much the same as that observed for surface chlorophyll concentrations, but the range of variations was less.

Variations in netplankton and nannoplankton chlorophyll content of the water column were also similar to the surface pattern. Nannoplankton chlorophyll-a values fluctuated between the low of 9.6 mg m^{-2} observed during the Oceanic Period and the high of 44.2 observed during the Mixed Period. Water column levels of netplankton chlorophyll-a, however, were less than 8.0 during the Oceanic Period and surpassed 110 during both strong upwelling pulses. Again, changes in the phytoplankton chlorophyll content of the water column and in the net/nanno ratio were due primarily to variations in the netplankton fraction with the nannoplankton fraction remaining comparatively constant (Table 2).

The vertical distribution of chlorophyll-a always exhibited a maximum which was in the photic zone above or in association with the phaeopigment maximum. The netplankton maximum was always located below the nannoplankton maximum except during strong upwelling when both maxima occurred in the upper 10 m of the photic zone (Figure 6). Four stations have been selected to illustrate the different types of vertical pigment distributions encountered (Figure 7). Two basic patterns were observed, a stable oceanic distribution with low chlorophyll concentrations and low net/nanno ratios (Figure 7a), and an upwelling distribution with high chlorophyll concentrations and high net/nanno ratios (Figure 7b). Under oceanic conditions, the nannoplankton maximum was found in the upper half of the photic zone, near the bottom of the mixed layer and in nitrate-poor water

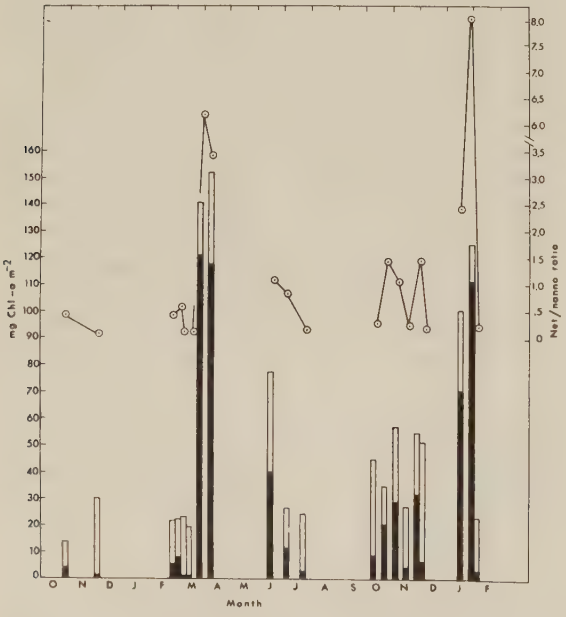


FIGURE 5.—Temporal variations in netplankton (■) and nannoplankton (□) chlorophyll-a content of the water column (mg m^{-2}, 0 to 100 m) and the net/nanno ratio (⊙) at CalCOFI 3.

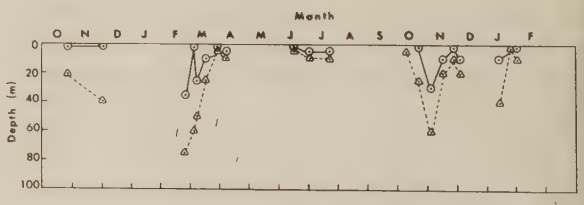


FIGURE 6.—Temporal variations in the depths of the nannoplankton (⊙) and netplankton (△) chlorophyll-a maxima at CalCOFI 3.

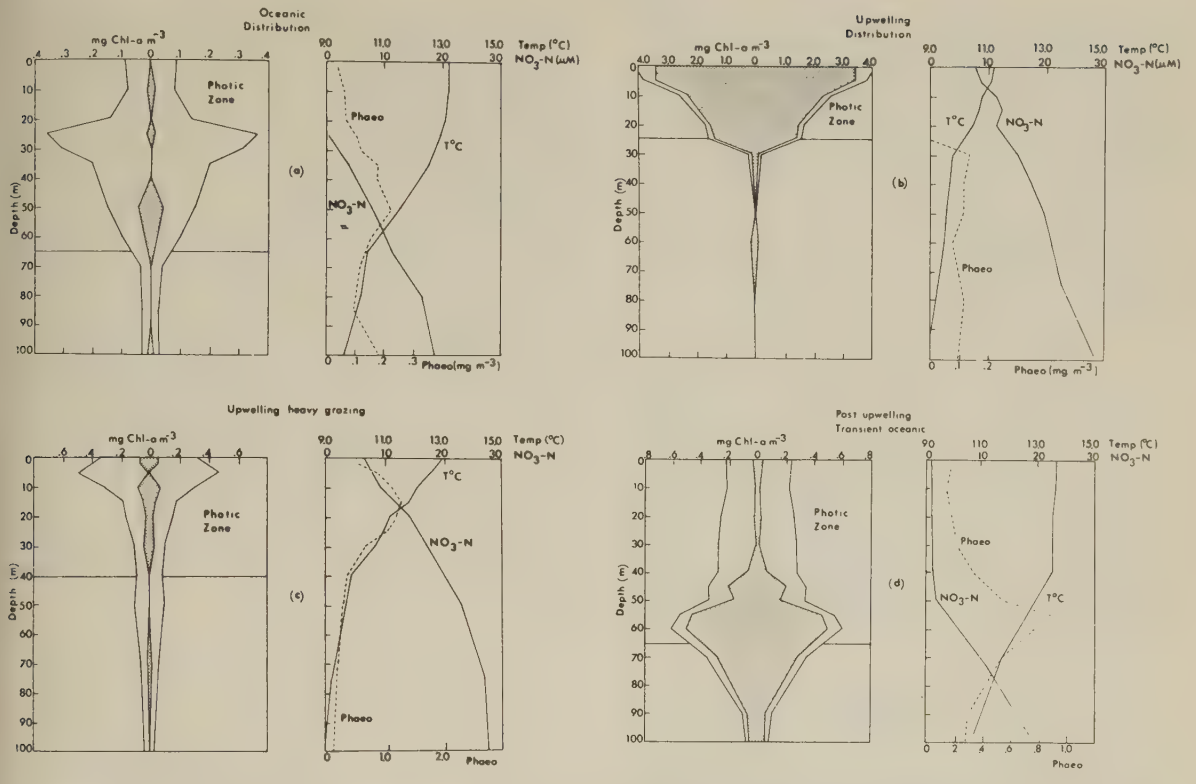


FIGURE 7.—Vertical profiles of netplankton (□) and nannoplankton (□) chlorophyll-a (mg m^{-3}), NO_3-N (μM), and temperature (°C) at CalCOFI 3: (a) Oceanic Period (10 March), (b) Upwelling Period (31 March), (c) Upwelling Period with peak grazing pressure (26 July), and (d) Mixed Period during post-upwelling subsidence (6 November).

(<0.5 μM NO_3-N); while the netplankton maximum was located in the lower half of the photic zone, in the thermocline, and in nitrate-rich water (>5.0 μM NO_3-N). Maximum phaeopigment concentrations occurred in association with or just below the netplankton maximum. With the onset of upwelling, the netplankton maximum gradually shifted from a depth of 75 m to the surface (Figure 6). Initially, upwelling had a dilution effect which was followed by a rapid increase in the netplankton fraction and later by a slight increase in the nannoplankton fraction (Figure 5). The upwelling distribution observed on March 31 is shown in Figure 7b. Both netplankton and nannoplankton chlorophyll maxima were at the surface and nitrate concentrations were high (>5.0 μM NO_3-N) throughout the photic zone.

The remaining two examples represent special cases which evolved from an upwelling distribution such as the one just described. Figure 7c shows the distribution observed during late July that developed over the period of steady upwelling during which the grazing pressure index increased markedly (Figure 3). Note that both netplankton and nannoplankton maxima were in the upper 10 m, and NO_3-N concentrations were in excess of 5 μM throughout the photic zone; but that the concentration of netplankton chlorophyll has been greatly reduced and the net/nanno ratio was low. Phaeopigments were high with a maximum just below the netplankton chlorophyll maximum. The distribution shown in Figure 7d (November 6) developed during a period of subsidence following an upwelling pulse. At this time, the netplankton maximum

was near the bottom of the photic zone 30 m below the nannoplankton maximum; the net-plankton chlorophyll concentration and net/nanno ratio were still high; and NO_3-N concentrations were greater than 2 μM throughout most of the photic zone.

GEOGRAPHIC VARIATIONS IN THE CALIFORNIA CURRENT

ENVIRONMENTAL FACTORS

Four transects across the core of the Current were made for this study (Figure 1). Transects 1-A, 2, and 3 were made during late July and August 1970, and transect 1-B was made during the first week of November 1970. CalCOFI station 3 in Monterey Bay was the inshore station for transects 1-A and B. The hydrographic conditions observed along these transects are summarized in Table 3 and Figures 8 and 9.

The July-August transects were made during a period of coastal upwelling and were characterized by shoreward rising isotherms and nitrate isopleths. Based on the upward slope of these isopleths, upwelling was least intense at the southernmost inshore station and most intense at the northernmost station, which is typical for this time of year (Reid et al., 1958). Nitrate concentrations were high in the upper half of the photic zone at the three inshore stations and low at the two outermost stations of each transect. Ammonium concentrations were relatively high (>1 μM NH_4-N) in the photic zone at the stations of transect 1-A but were low (typically 0.1 to 0.5 μM) throughout the water column at most of the remaining stations. The surface mixed layer was never observed to extend below the photic zone, inshore or offshore. An undercurrent was present below the thermocline between stations 5 and 8 of transect 1-A as indicated by the spreading isotherms (cf. Wooster and Gilmartin, 1961). Based on the temperature (Figure 8) and nitrate profiles (Figure 9), the stations along each transect were divided into three groups:

1. Stations within about 100 km of the coast were classified as inshore (stations 3, 61, and 63),
2. Stations between 100 and 250 km offshore were classified as transitional (stations 8, 55, and 67),

TABLE 3.—Environmental factors monitored concurrently with measurements of productivity and standing crop in the California Current system between lat 35° and 50° N.

Station	Date	Distance from land	Temperature	Salinity	NO_3-N	NH_4-N	Mixed layer	Photic zone
		km	°C	‰	μM	μM	m	m
03a	26 July 70	15	12.95	33.82	6.5	3.3	0	40
08	27 July	155	14.88	33.11	1.3	1.4	20	65
15	29 July	470	17.69	32.95	0.2	1.8	30	105
24	31 July	675	18.49	32.88	0.1	1.7	20	100
33	2 Aug.	535	18.03	32.51	0.0	0.4	0	115
61	9 Aug.	30	11.98	33.38	8.8	0.7	10	40
55	7 Aug.	130	16.04	31.88	0.1	0.0	10	65
46	5 Aug.	310	17.25	32.08	0.1	0.4	15	105
38	3 Aug.	485	18.25	32.79	0.1	0.3	15	95
63	15 Aug.	70	11.55	33.00	0.3	0.5	10	15
67	16 Aug.	150	14.91	32.62	0.7	0.2	30	75
73	18 Aug.	315	17.24	32.04	0.1	0.5	20	55
84	20 Aug.	450	17.07	32.57	0.2	0.1	30	90
88	22 Aug.	280	15.82	32.47	0.1	0.3	20	80
03a	6 Nov.	15	13.59	32.99	0.7	0.2	40	60
14	5 Nov.	90	14.58	32.98	0.0	0.5	20	65
05	2 Nov.	150	14.38	32.81	0.1	0.7	20	50
12	4 Nov.	225	14.74	32.62	0.2	0.1	15	60
08	3 Nov.	290	15.31	32.46	0.1	1.0	15	60

a CalCOFI station 3.

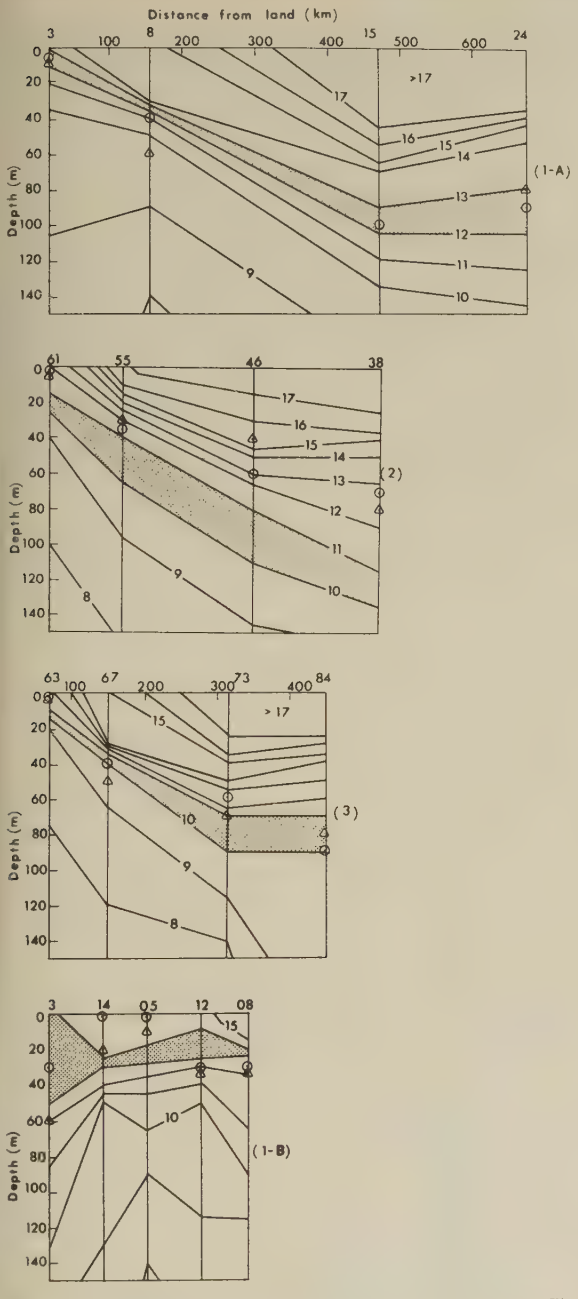


FIGURE 8.—Vertical distribution of temperature (°C) along four transects of the California Current system with the depths of the nannoplankton (⊙) and netplankton (△) chlorophyll-a maxima: (1-A) along lat 37° N in July, (2) along lat 40° N in August, (3) along lat 44° N in August, and 1-B along lat 36°40' in November. Vertical lines represent stations.

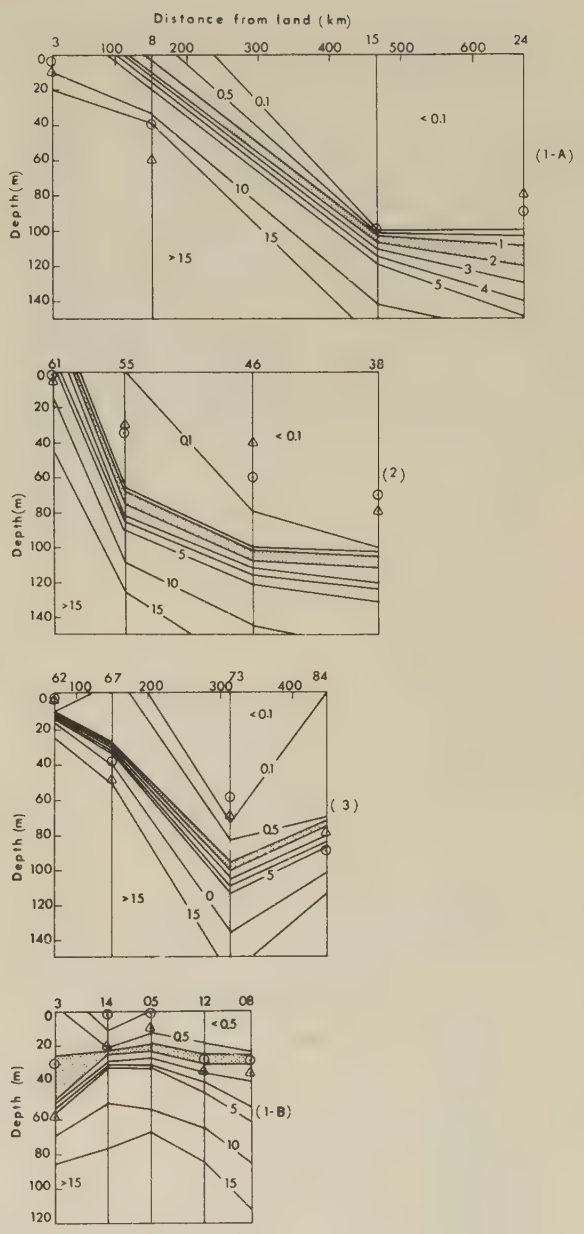


FIGURE 9.—Vertical distribution of NO_3-N (μM) along four transects of the California Current system with the depths of the nannoplankton (⊙) and netplankton (△) chlorophyll-a maxima.

3. Stations greater than 250 km from the coast were classified as offshore (stations 15, 24, 33, 46, 38, 73, 84, and 88).

Transect 1-B was made at a time when the Davidson Current is usually developed (Bolin, 1964). The inshore station (CalCOFI 3) was occupied during an oceanic phase of the Mixed Period, and subsidence is evidenced by the downward trend of the isotherms and nitrate isopleths (Figures 2, 8, and 9). Surface temperatures were comparatively high and nitrate concentrations low. The Davidson Current was developed at stations 3 and 14, and the transition from Davidson to California Current Water occurred between stations 14 and 12 with a surface divergence probably located between stations 5 and 12. Station 8, the outermost station, was in the California Current proper.

SURFACE PRIMARY PRODUCTIVITY AND STANDING CROP

During the July-August transects, when coastal upwelling dominated the hydrographic regime of the California Current system, phytoplankton productivity and chlorophyll-a concentrations decreased markedly with distance from land (Figure 10). Inshore, productivity and chlorophyll ranged from 6.62 to 61.65 mgC m^{-3} hr^{-1} and from 0.8 to 11.5 mg m^{-3}, respectively. Pro-

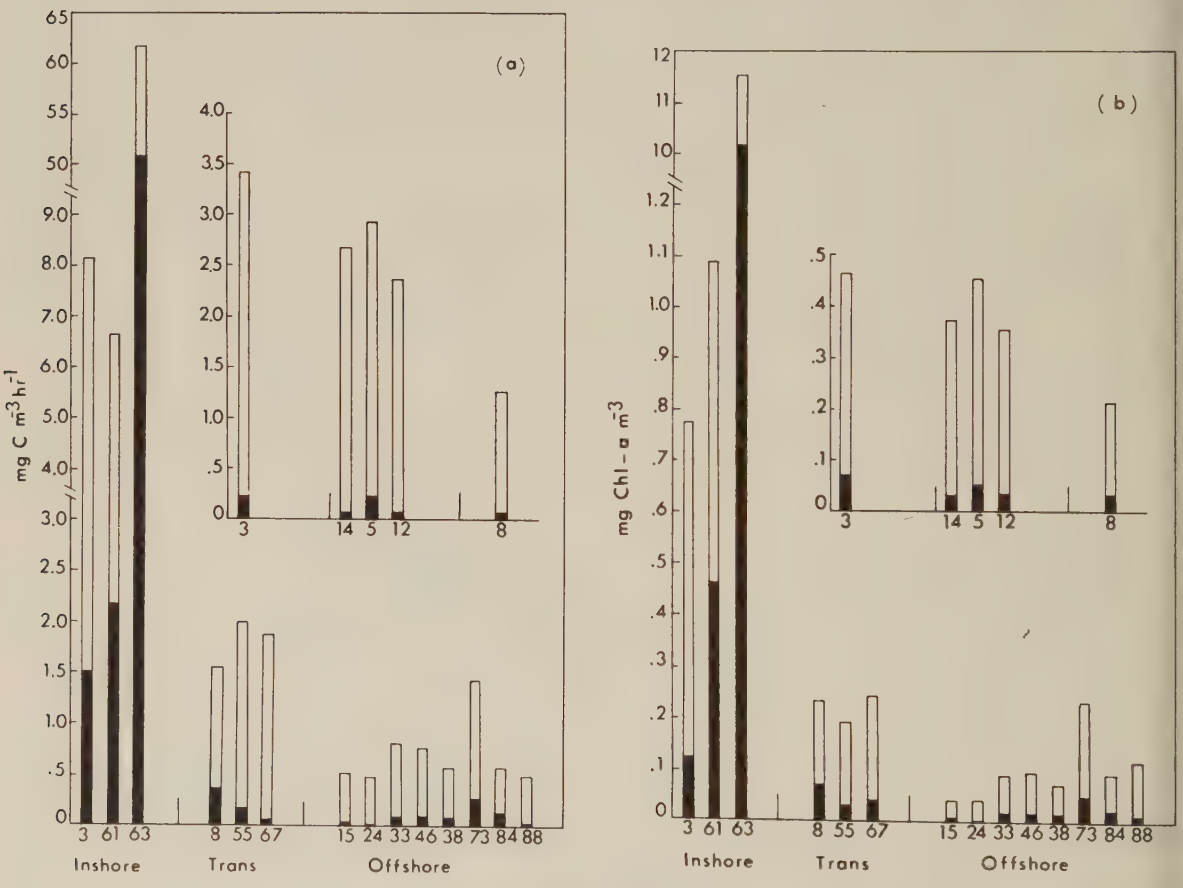


FIGURE 10.—a. Inshore-offshore variations in surface netplankton (■) and nannoplankton (□) productivity (mgC m^{-3} hr^{-1}) during the July-August transects and the November transect (inset). b. Inshore-offshore variations in surface netplankton and nannoplankton chlorophyll-a (mg m^{-3}).

ductivity and chlorophyll concentrations offshore, however, exceeded 1.0 mgC m^{-3} hr^{-1} and 0.10 mgChl-a m^{-3} only once. The highest levels of productivity and chlorophyll were found at inshore station 63 and were equivalent to the maximum values observed at CalCOFI 3 during the two most intense upwelling pulses.

This inshore-offshore decrease in surface productivity and chlorophyll was not observed over the first 225 km of the November transect when subsidence rather than upwelling characterized. the coastal hydrographic regime. Productivity and chlorophyll concentrations were relatively constant out to station 12 (Figure 10) and corresponded with the minimum values observed at CalCOFI 3 during the Oceanic Period.

Both nannoplankton and netplankton productivity and chlorophyll decreased markedly between inshore and offshore stations along the July-August transects (Figure 10). Nannoplankton values fell by as much as an order of magnitude from above 4.0 mgC m^{-3} hr^{-1} and 0.60 mgChl-a m^{-3} to less than 1.2 and 0.18, respectively. The netplankton, however, exhibited the greatest decline. Netplankton productivity decreased by 2 to 3 orders of magnitude from 1.5 to 51.3 mgC m^{-3} hr^{-1} to offshore levels of 0.01 to 0.26. Similarly, netplankton chlorophyll values were 0.12 to 10.14 mg m^{-3} inshore and 0.002 to 0.052 offshore. This decline in the netplankton fraction relative to the nannoplankton is reflected in the net/nanno ratios (Table 4). Inshore productivity ratios ranged from 0.23 to 4.95, while offshore ratios varied from 0.02 to 0.36. Chlorophyll ratios followed the same pattern but tended to be higher.

The pattern observed in November was quite different. Levels of netplankton productivity and chlorophyll were low along the entire transect and were within the range commonly found offshore and during oceanic phases inshore (Figure 10). Nannoplankton productivity declined slightly from an inshore maximum of 3.20 to an offshore minimum of 1.21. Variations in surface chlorophyll were similar except the maximum of 0.40 was observed at station 5 which is 150 km from shore. Station 5 is particularly interesting because netplankton productivity and chlorophyll also exhibited small peaks here, and it was located near the boundary between the Davidson and California Currents which is marked by a surface divergence and associated upwelling. In this connection, it is also noteworthy that nannoplankton productivity and chlorophyll levels were about twice those observed previously for transitional and offshore regions.

Phytoplankton assimilation ratios were similar to those observed at CalCOFI 3, most values falling between 5 and 10. Excluding inshore stations, the mean assimilation ratio was 7.7 ± 1.1, which is not significantly different from the mean observed at CalCOFI 3. Nannoplankton ratios averaged 8.3 ± 1.2 which is twice the observed mean netplankton ratio of 4.1 ± 0.8. Both means are equivalent to those observed at CalCOFI 3.

VERTICAL DISTRIBUTION OF PIGMENTS

Inshore-offshore variations in the chlorophyll-a content of the water column (0 to 200 m) during the July-August transects were similar in trend but less in amplitude than that observed at the surface. Inshore, chlorophyll varied from 27.32 to 217.68 mg m^{-2} compared with the

TABLE 4.—Netplankton-nannoplankton ratios in the California Current system: primary productivity (PP = mgC m^{-3} hr^{-1}), chlorophyll-a m^{-3}, and chlorophyll-a m^{-2}.

Station	PP	m^{-3}	m^{-2}
03	0.23	0.18	0.14
08	0.30	0.48	0.36
15	0.06	0.15	0.21
24	0.02	0.05	0.14
33	0.11	0.22	0.06
61	0.49	0.75	0.75
55	0.09	0.19	0.16
46	0.12	0.22	0.31
38	0.19	0.27	0.24
63	4.95	7.31	5.82
67	0.03	0.18	0.33
73	0.22	0.28	0.22
84	0.36	0.32	0.14
88	0.07	0.09	0.09
03	0.07	0.17	1.12
14	0.02	0.10	0.18
05	0.08	0.12	0.20
12	0.03	0.11	0.10
08	0.04	0.17	0.16

offshore range of 10.72 to 25.96 mg m^{-2} (Figure 11). In November the pattern was much the same, with an inshore maximum of 66.64 and an offshore level of 23.20.

Nannoplankton chlorophyll in the water column showed little variability (Figure 11). Inshore levels of nannoplankton chlorophyll varied from 17.49 to 31.94 mg m^{-2}, while offshore levels ranged between 9.63 and 21.76. The netplankton fraction underwent much greater fluctuations (Figure 11). Inshore concentrations ranged between 3.26 and 185.74 in contrast to the offshore range of 1.00 to 4.97. The latter range is equivalent to that observed at CalCOFI 3 during the Oceanic Period and the former to that observed during the Upwelling Period. Excluding inshore stations, the mean chlorophyll-a concentration of the nannoplankton fraction was 16.55 ± 2.38 which is significantly higher ($P = 0.05$) than the netplankton mean of 3.08 ± 0.81.

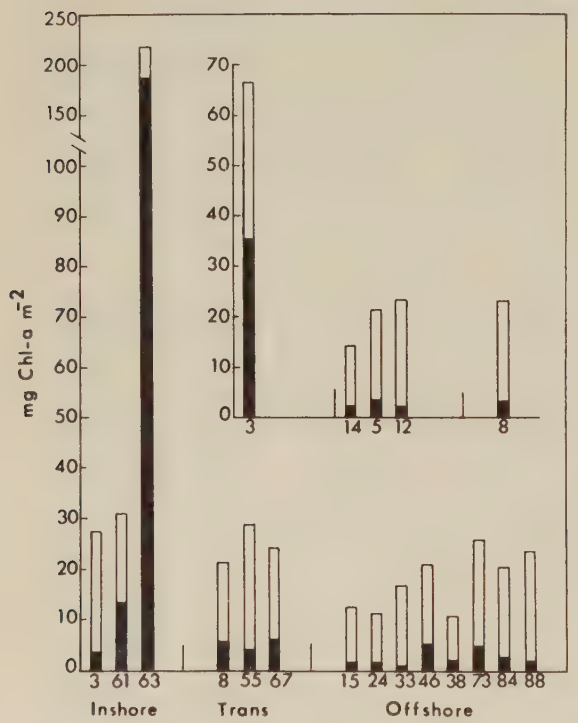


FIGURE 11.—Inshore-offshore variations in the netplankton (■) and nannoplankton (□) chlorophyll-a content of the water column (mg m^{-2}, 0 to 200 m) during the July-August transects and the November transect (inset).

The vertical distributions of chlorophyll-a and phaeopigments at the offshore stations of the July-August transects were characterized by a subsurface maximum located at the base of the photic zone, in the lower part of the thermocline, and near the upper reaches of the nitrate-rich layer (Figure 12). Netplankton and nannoplankton chlorophyll maxima were usually located near each other, but the netplankton maximum was not always deeper than the nannoplankton maximum. Netplankton chlorophyll was more evenly distributed and concentrations were much lower than in inshore waters (compare Figures 7 and 12). Both maxima gradually decreased in depth shoreward from between 80 and 100 m offshore to 10 m or less at the inshore stations paralleling the upward trend of the isotherms (Figure 8) and nitrate isopleths (Figure 9).

The pattern was much different during the November transect (1-B). The netplankton maximum was always located below the nannoplankton maximum, especially at the inshore station where the netplankton maximum was 30 m below the nannoplankton maximum (Figure 7d). Both maxima decreased in depth seaward to station 5 (Figures 8 and 9) where the vertical distribution conformed to the upwelling distribution (Figure 12), i.e., netplankton and nannoplankton maxima were in the upper 10 m and nitrate concentrations were relatively high throughout most of the photic zone. Farther offshore the depth of the chlorophyll maxima increased once again. This up and down movement of the maxima closely paralleled the depth variation of the isotherms and nitrate isopleths just as during the July-August transects.

DISCUSSION

The constancy of the phytoplankton assimilation ratios both inshore (7.4 ± 1.0) and offshore (7.7 ± 1.1) suggests that nutrients were rarely limiting to primary productivity (Dickman, 1969). The mean assimilation ratios found are close to the value of 7.3 reported by Holmes (1958b) in the nutrient-rich waters of the Costa

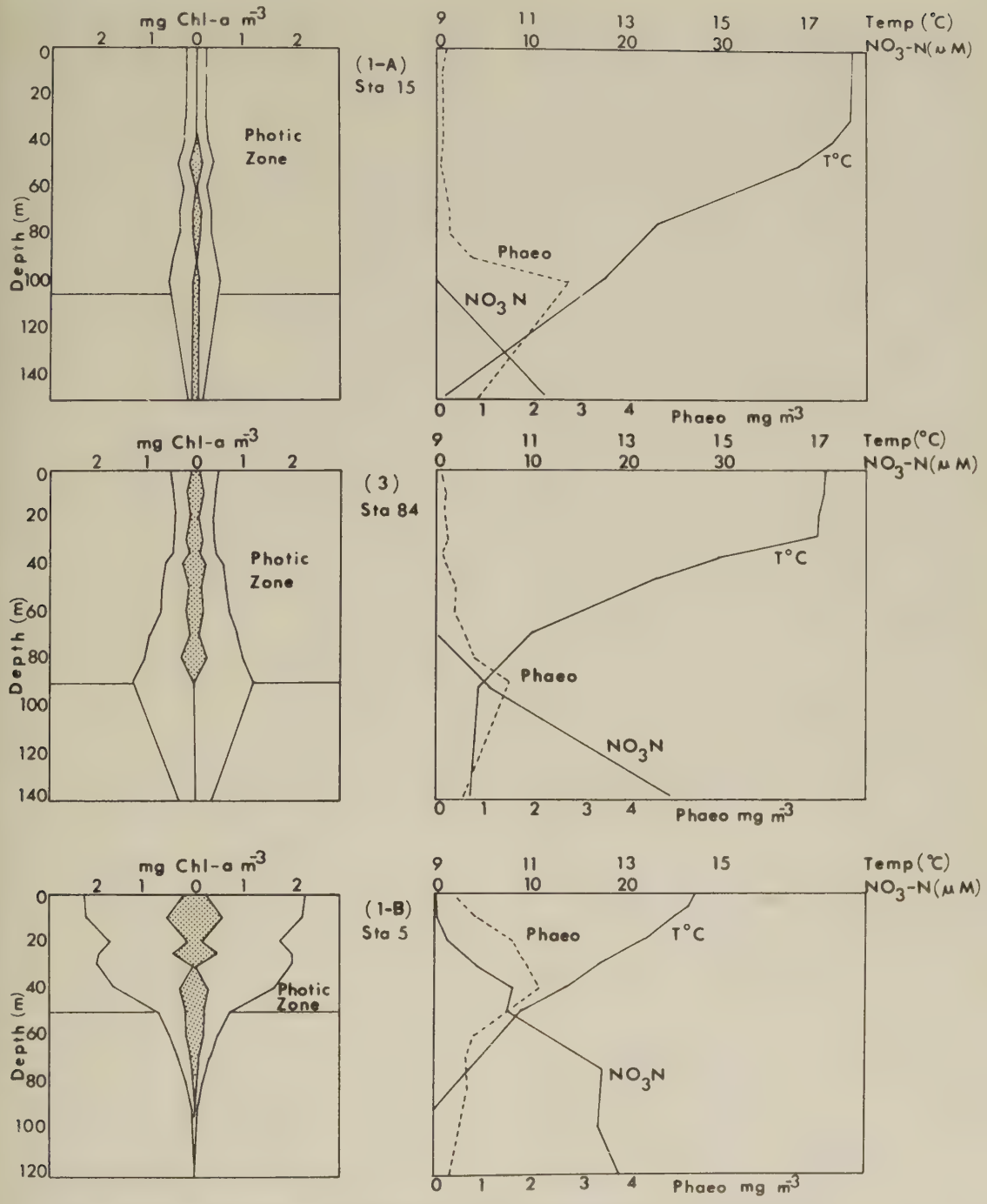


FIGURE 12.—Vertical profiles of netplankton (▫) and nannoplankton (□) chlorophyll-a (mg m^{-3}), phaeopigments (mg m^{-3}), NO_3-N (μM), and temperature (°C): transect 1-A, station 15, offshore region; transect 3, station 84, offshore; transect 1-B, station 5, transition zone.

Rica Dome (incubator light intensity about 0.06 langley/min) and are not significantly different from the mean of 8.6 ± 1.3 found by Curl and Small (1965) at light saturation based on in situ measurements. Anderson (1964), working off the Washington and Oregon coasts, obtained ratios of 1.6 to 9.8 (at about 0.02 langley/min) with low values occurring during the summer when nutrient concentrations were low and high values during the spring bloom when nutrient concentrations were high. In the eastern tropical Pacific, Thomas (1970) and Malone (in press a) found that assimilation ratios were significantly less in nitrogen-poor than in nitrogen-rich waters. These results are consistent with the observations of Curl and Small (1965), supported by McAllister et al. (1964), which suggest that ratios below 3 are indicative of a nutrient deficiency while those above 5 indicate nutrient-rich waters.

Both the nannoplankton and the netplankton exhibited relatively constant assimilation ratios, but mean nannoplankton ratios were significantly higher (9.4 ± 1.5 inshore, 8.3 ± 1.2 offshore) and twice as great as those of the netplankton (4.7 ± 1.3 inshore, 4.1 ± 0.8 offshore). The constancy of these ratios over a wide range of productivity values in spite of large variations in ambient nitrogen concentrations indicates that nutrient concentration was not an important limiting factor and that the phytoplankton were adapted to about the same light intensity over the entire year. This is conceivable since seasonal variations in day length and light intensity tend to be dampened by the seasonal pattern of cloud coverage, i.e., the summer months are usually foggy while the winter months are usually clear. The situation is similar to that found off La Jolla (Strickland et al., 1970).

Increases in the productivity and standing crop of the netplankton fraction and in the net/nanno ratio were closely coupled with the occurrence of upwelling. Each new upwelling pulse, regardless of duration (CalCOFI 3) or location (transect 1-B) was marked by an increase in net/nanno ratios and netplankton standing crop. Potentially, upwelling can affect phytoplankton productivity in at least two ways: (1) by increasing the residence time of cells in the upper reaches of the photic zone and (2) by increasing the rate at which nutrients are supplied to the photic zone. The settling velocities of phytoplankton cells range between 0 and 10 m day^{-1} (for a review see Smayda, 1970), with most values falling between 0.5 and 2 m day^{-1} (Eppley et al., 1967; Strickland et al., 1969). Average upwelling velocities are of the order of 10 m day^{-1} (Hidaka, 1954), which is quite sufficient to inhibit the sinking of negatively buoyant cells.

Since the netplankton fraction was primarily composed of nonmotile diatoms and the nannoplankton fraction of flagellates, it is probable that vertical water movements will have a greater effect on the vertical distribution of netplankton than on the nannoplankton. It is not surprising, therefore, that the depth of the netplankton maximum was more closely tied to the upward and downward trends of the isotherms, both seasonally at CalCOFI 3 (Figure 6) and along inshore-offshore transects of the California Current (Figure 8). The netplankton maximum at CalCOFI 3 was always found below that of the nannoplankton except during strong upwelling when both maxima occurred in the upper 10 m. During periods of subsidence the netplankton minimum was depressed to greater depths than the nannoplankton maximum was. This was observed during the Mixed Period even though NO_3-N concentrations in the surface layers were still high (>1.0 μM). The reverse was observed along transect 1-B in that the netplankton maximum decreased in depth as the zone of offshore upwelling was approached, moving in the process from a nitrate-rich layer (>5.0 μM NO_3-N) into a nitrate-poor layer (<0.5 μM NO_3-N). The depth distribution of nannoplankton chlorophyll (Figures 6 and 7) was more independent of vertical water movements and maximum chlorophyll concentrations were often found at the surface during influxes of oceanic water (during both Oceanic and Mixed Periods) when subsidence was most pronounced.

Most of these trends in the depth distribution of netplankton and nannoplankton chlorophyll could be explained in terms of the vertical distribution of nitrate in the photic zone. However, during the early stages of upwelling in

March, the netplankton maximum moved progressively toward the surface while the chlorophyll concentration of the maximum and in the water column steadily decreased. If this change in depth was due solely to the upward movement of the nitrate-rich layer in the photic zone, some increase in netplankton would have been observed during the time taken for the maximum to move from a depth of 75 m to 5 m. In addition, measurements made in the Peru Current, where vertical advection was not in evidence and the photic zone was well stratified (Malone, in press a), support the hypothesis that upward water movements, in addition to high nitrate concentrations, are necessary prerequisites for netplankton productivity to approach or exceed that of the nannoplankton. Netplankton productivity and the net/nanno productivity ratio were low despite high nitrate concentrations (Figure 13).

Two lines of evidence indicate that the netplankton and nannoplankton respond differently to varying nitrate concentrations. The first is based on the relationship between productivity and nitrate concentrations encountered in different environments (Figure 13). Nannoplankton productivity increased rapidly as NO_3-N increased from about 0.0 to 0.5 μM. Above 0.5 μM nannoplankton productivity increased asymptotically. In contrast, netplankton productivity increased slowly over concentrations of 0.0 to 1.5 μM and then increased rapidly with concentrations in excess of 1.5 μM (California Current system). The netplankton, therefore, tend to have higher half-saturation constants and maximum uptake rates for nitrate than the nannoplankton, so that NO_3-N concentrations above 1 to 3 μM are necessary before the netplankton can effectively compete with the nannoplankton. This agrees with the results of MacIsaac and Dugdale (1969) and Eppley et al. (1969), which indicate that small-celled oceanic species in oligotrophic waters have K_s values for nitrate uptake of less than 0.5 μM while large-celled neritic species in eutrophic waters have K_s values greater than 1.0 μM.

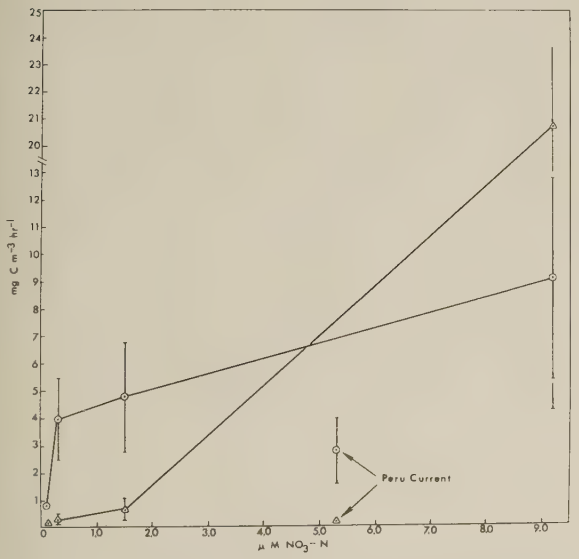


FIGURE 13.—Mean netplankton (△) and nannoplankton (⊙) productivity as a function of mean NO_3-N concentrations with 95% confidence limits: 0.1 μM, offshore oceanic region; 0.3 μM, CalCOFI 3, Oceanic Period; 1.5 μM, CalCOFI 3, Mixed Period; 9.2 μM, inshore upwelling.

The observed inshore vertical distributions of netplankton and nannoplankton chlorophyll were also consistent with these observations. The netplankton chlorophyll maximum was always found at depths where NO_3-N concentrations were greater than 2 μM, while during nonupwelling periods (when concentrations less than 2 μM were found in the photic zone) the nannoplankton maximum occurred at depths where the NO_3-N concentration was between 0.2 and 2.0 μM. Similar observations were made by Eppley (1970) who found that diatoms were associated with relatively high nitrate concentrations at depths where light intensities were high enough for growth to occur.

Based on these observations, netplankton productivity and standing crop will increase relative to the nannoplankton only when NO_3-N concentrations above 1 to 3 μM are found in the upper half of the photic zone and when the netplankton standing crop is supported in the photic zone by vertical advection, i.e., upwelling.

Decreases in netplankton standing crop and net/nanno ratios were related to influxes of oceanic water and increases in grazing pressure in Monterey Bay. Variations in phytoplankton

productivity and grazing conformed to what Cushing (1959) has referred to as an unbalanced seasonal cycle of primary production and primary consumption. Neritic regions in temperate waters are generally characterized by about a 2-month time interval between peaks in phytoplankton and zooplankton biomass (Cushing, 1959; Heinrich, 1962), with a time lag of about 1 month between the onset of the spring bloom and the increase in zooplankton standing crop. Martin (1965) found a 2-month lag between the maximum phytoplankton standing crop and the increase in zooplankton standing stock.

In Monterey Bay, about 2 months elapsed between the March-April phytoplankton bloom and the rapid increase in grazing pressure observed during June and July (Figure 3). Although upwelling was in progress (NO_3-N concentrations were greater than 5 μM throughout the photic zone and the netplankton chlorophyll maximum was in the upper 10 m), the phytoplankton chlorophyll content of the water column declined as grazing pressure increased. The netplankton fraction fell continuously while the nannoplankton dropped at first and then increased (Figure 5). The reduction in standing crop was accompanied by a steady decline in the ratio of netplankton-to-nannoplankton chlorophyll in the water column, from 1.1 near the beginning of the increase in grazing pressure to 0.1 at its peak. Thus, it appears that (1) the phytoplankton bloom was ultimately limited by grazing; (2) the netplankton fraction, dominated by *Nitzschia* spp. and *Rhizosolenia* spp. (80% of the netplankton by number), was selectively grazed; and (3) the cycle of netplankton production and animal grazing was unbalanced.

Variations in the net/nanno chlorophyll m^{-2} ratio were significantly related to concurrent changes in the nitrate content of the photic zone (an indicator of upwelling) and to grazing pressure ($F = 5.56$, $P = 0.05$) by the multiple regression equation:

$$\text{net/nanno} = 1.76 + 0.003\ (NO_3\text{-N}) - 2.53\ (\text{Phaeo/Chl-a}).$$

This equation is based on 20 sets of data (CalCOFI 3), and the partial correlation coefficients for the interactions between the net/nanno ratio and nitrate concentration ($r = +0.51$) and between the ratio and grazing pressure ($r = -0.56$) are significant at the 0.05 level. The evidence suggests, therefore, that upwelling is a necessary precondition for netplankton productivity and standing crop to approach or exceed that of the nannoplankton in marine environments where water depth greatly exceeds the maximum depth of wind-driven turbulent mixing.

The relative constancy of the nannoplankton relative to the netplankton fraction, in spite of marked changes in the concentration of inorganic nitrogen, the intensity and direction of vertical water movements, and grazing pressure, is puzzling. The assimilation ratios of both fractions exhibited little variability, but on the average nannoplankton ratios were twice as great as those of the netplankton. Since this ratio is an index of growth rate (cf. Eppley and Strickland, 1968), the nannoplankton must have been limited primarily by "cropping" factors (Dickman, 1969), at least during those periods when netplankton productivity was increasing relative to nannoplankton productivity. This is supported by the observation that the chlorophyll content of nannoplankton and netplankton cells also exhibited little variability during the period of study. During upwelling, two processes could selectively remove nannoplankton cells from upwelling regions: (1) grazing and (2) horizontal advection.

If nannoplankton grazers were predominantly protozoans (Beers and Stewart, 1969) with short generation times and netplankton grazers were crustaceans and fishes with long generation times, the coupling between primary productivity and grazing would be much closer for nannoplankton-based food chains than for netplankton-based food chains. The cycle of nannoplankton productivity and animal grazing would be balanced (Cushing, 1959; Heinrich, 1962) in contrast to the unbalanced character of netplankton-based food chains. This would tend to dampen fluctuations in the nannoplankton fraction relative to the netplankton fraction.

Similarly, if nannoplankton cells were selectively removed from sites of upwelling by mass

transport normal to the coast because of their lower sinking rates, netplankton cells would have a greater tendency to remain closer to the region of upward water movement than nannoplankton cells (Stommel, 1949). Both of these processes, selective grazing by organisms with short generation times and horizontal advection away from upwelling sites, would limit increases in nannoplankton standing crop during upwelling and could compensate for the growth rate differential between the netplankton and nannoplankton fractions. This would set the stage for netplankton productivity and standing crop to exceed that of the nannoplankton during upwelling, and also explain the discrepancy between nannoplankton growth rates and their response to photic zone enrichment. Decreases in nannoplankton standing crop due to "excessive" grazing or removal from the photic zone by downward water movements would be dampened by the short generation times (and, therefore, potentially rapid response time) and motility of the nannoplankton species.

Comparisons of the Oceanic Period in Monterey Bay with the offshore oceanic environment of the California Current reveals an interesting pattern of netplankton and nannoplankton variation which is consistent with the above model. The productivity and standing crop of the netplankton fraction did not vary significantly between the Oceanic Period inshore and the offshore oceanic zone. In contrast, the nannoplankton were significantly higher inshore than offshore (Table 5). This "inshore enhancement" effect during intrusions of oceanic water could arise in response to the overall pattern of circulation. The vertical distribution of nannoplankton chlorophyll compared with that of the netplankton indicated that nannoplankters are more independent of vertical water movements and are better able to maintain their position in the water column. This ability, probably a consequence of motility, will result in a concentration of nannoplankton in regions of downward flow (Hutchinson, 1967). In addition, the ability of nannoplankton to maintain their position in the photic zone could give rise to a situation analogous to the "island mass effect" described by Doty and Oguri (1956). The former is more likely, however, since assimilation ratios were equivalent in both inshore and offshore environments, i.e., the increase in primary productivity was a consequence of higher standing crops rather than an increase in growth rates.

TABLE 5.—Mean netplankton and nannoplankton productivity and standing crop with 95% confidence limits for the Oceanic Period at CalCOFI 3 and the offshore oceanic region of the California Current.

Oceanic region	Measurement	Nanno		Net	
Offshore	mgC m^{-3} hr^{-1}	0.69 ± 0.20		0.08 ± 0.05	
Inshore		3.90	1.53	0.25	0.20
Offshore	mgChl-a m^{-3}	0.093	0.036	0.019	0.010
Inshore		0.477	0.227	0.068	0.047
Offshore	mgChl-a m^{-2}	15.60	3.22	2.58	0.92
Inshore		18.14	5.15	3.71	2.17

SUMMARY AND CONCLUSIONS

Phytoplankton productivity and standing crop were low under oceanic conditions, both inshore and offshore. During the Oceanic Period in Monterey Bay the nannoplankton accounted for 60 to 99% of the observed productivity and standing crop, while offshore this fraction was responsible for 75 to 99%. The productivity and standing crop of the netplankton fraction were exceedingly low and constant under these conditions, but the nannoplankton fraction was significantly higher inshore than offshore. Netplankton productivity and standing crop exceeded that of the nannoplankton only during periods of strong upwelling.

The netplankton fraction was composed almost exclusively of diatoms while the nannoplankton fraction was dominated by flagellates. Similar, but more detailed observations off La Jolla, Calif., (Reid et al., 1970) showed the nannoplankton to be composed primarily of naked dinoflagellates, "monads" (e.g., *Chilomonas marina* and *Eutreptia* sp.), and coccolithophores (e.g., *Coccolithus huxleyi*).

The nannoplankton fraction was surprisingly stable both seasonally in Monterey Bay and geographically in the California Current system. Variations in phytoplankton productivity and standing crop were due primarily to the netplankton with the nannoplankton maintaining a comparatively stable background level.

Increases in netplankton productivity and standing crop were closely related to upwelling, both as a consequence of the positive vertical advection and the entrainment of nitrate into the upper half of the photic zone. The requirement for positive vertical advection was probably related to both cell size and motility so that the vertical distribution of nannoplankters was more independent of vertical water movements. The relationship between cell size and A/V ratios probably accounted for the higher nitrate requirements of the netplankton. Decreases in the netplankton were primarily due to grazing and to removal from the photic zone by downward water movements.

The stability of the nannoplankton compared to the variability of the netplankton is interesting, especially in light of the marked changes observed in the concentration of inorganic nitrogen compounds and the direction and intensity of vertical water movements. Since nannoplankton assimilation ratios were consistently high and twice as great as netplankton assimilation ratios, the nannoplankton must have been limited primarily by cropping factors during upwelling periods when netplankton standing crop was increasing relative to that of the nannoplankton. Under these conditions increases in the nannoplankton fraction will be dampened by selective removal from upwelling sites by mass transport away from the coast and grazing by organisms with short generation times (e.g., protozoans). Decreases in nannoplankton standing crop due to "excessive" grazing or removal from the photic zone by downward water movements will be limited by the motility and short generation times of nannoplankton species. The motility of nannoplankters in combination with onshore mass transport and downward water movements will also favor an offshore-inshore increase in nannoplankton productivity and standing crop.

Finally, it is clear that the nannoplankton and netplankton components of phytoplankton communities respond differently to changes in their environment; that cell size, surface-to-volume ratios, and motility play important roles in mediating these responses; and that changes in netplankton and nannoplankton productivity relative to each other have definite consequences with respect to energy flow through phytoplankton-based food chains.

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DISTRIBUTION, APPARENT ABUNDANCE, AND LENGTH COMPOSITION OF JUVENILE ALBACORE, *Thunnus alalunga*, IN THE SOUTH PACIFIC OCEAN

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ABSTRACT

The distribution, apparent abundance, and length composition of juvenile albacore, *Thunnus alalunga*, were deduced from 127 specimens found in the stomachs of 2,297 billfishes collected in the South Pacific between January 1964 and July 1966. Juvenile albacore were found in the South Pacific from lat 5° to 31° S, between long 153° and 179° W. Billfish stomach samples were collected from as far east as long 135° W, but juveniles were not in the stomachs east of long 153° W. The juveniles were consistently more numerous between lat 10° and 20° S than in the area farther north. The mean length of the juveniles increased from north to south but not from east to west (or vice versa). A southward migration of juveniles is postulated.

In April 1963, the National Marine Fisheries Service (formerly the Bureau of Commercial Fisheries), Hawaii Area Fishery Research Center established a field station in Pago Pago, American Samoa, to collect information on the longline fishery based there. A fleet of vessels from Japan, the Republic of Korea, and the Republic of China has supplied two American-owned canneries with albacore, *Thunnus alalunga*, and other tuna. In 1965 the fleet was composed of 154 vessels which landed 15,588 metric tons of albacore (Otsu and Sumida, 1968).

The field station was established primarily to study the effects of the fishery on albacore. As part of this study an investigation was started to determine the early life history of albacore in the South Pacific.

Beginning in 1964, arrangements were made with several longline fishing vessels based in American Samoa to collect stomachs of billfishes, which are known to prey on juvenile tunas (Yoshida, 1965, 1968). The distribution, apparent abundance, and length composition of juvenile albacore, here defined as fish smaller than 400 mm standard length, were determined by specimens found in the stomachs of the predators.

MATERIALS AND METHODS

The longline vessels based at American Samoa fished primarily for albacore; billfishes were taken only incidentally. The crews of the cooperating longline vessels collected 2,297 billfish[2] stomachs between January 1964 and July 1966. These stomachs were also used in a study of juvenile skipjack tuna, *Katsuwonus pelamis* (Yoshida, 1971).

In the laboratory, all the tunas and tunalike specimens were first sorted from the stomach contents. The juvenile tunas were identified by the use of skeletal characters; juvenile albacore were easily identified by their definitive skeletal characters (Matsumoto, 1963; Yoshida, 1965). Standard length (SL) was taken for all intact juveniles and is the measurement used throughout. For fragmentary specimens, the standard length was estimated from previously determined relations between standard length and various vertebral segments (Yoshida, 1968). A total of 127 juvenile albacore was found in the billfish stomachs (Table 1).

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[2] For the purpose of this paper the term billfish, in addition to the Istiophoridae, includes the swordfish, *Xiphias gladius*.

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TABLE 1.—Juvenile albacore found in billfish stomachs from the South Pacific.

Date 1964	Position		Standard length	Date 1965	Position		Standard length	Date 1966	Position		Standard length
	Lat S	Long W			Lat S	Long W			Lat S	Long W	
			mm				mm				mm
3/9	07°00′	170°00′	143	1/5	14°00′	174°00′	122	1/7	15°00′	175°00′	107
3/20	06°00′	164°00′	116	1/5	14°00′	174°00′	97	1/9	15°00′	174°00′	89
3/21	05°00′	165°00′	67	1/22	14°00′	175°00′	96	1/9	15°00′	174°00′	83
4/4	08°00′	175°00′	102	1/22	14°00′	175°00′	78	1/9	16°00′	174°00′	110
4/5	08°00′	175°00′	136	1/22	14°00′	175°00′	84	1/9	16°00′	174°00′	113
4/9	07°00′	178°00′	78	1/24	14°00′	174°00′	102	1/9	16°00′	174°00′	133
4/9	07°00′	178°00′	137	1/25	14°00′	174°00′	109	1/17	12°00′	175°00′	106
4/12	07°00′	178°00′	26	1/26	11°00′	162°40′	81	1/23	12°40′	171°00′	133
4/16	07°00′	179°00′	57	1/27	14°00′	174°00′	118	2/8	09°00′	172°00′	130
4/19	07°00′	178°00′	102	1/29	14°00′	175°00′	110	2/8	09°00′	172°00′	137
4/20	07°00′	179°00′	66	1/30	14°00′	175°00′	102	2/8	09°00′	172°00′	130
4/20	07°00′	179°00′	66	4/4	07°10′	164°13′	123	2/8	09°00′	172°00′	93
4/20	07°00′	179°00′	106	4/12	07°10′	170°20′	102	2/13	07°02′	171°30′	102
4/24	09°00′	176°00′	115	4/22	07°00′	174°45′	86	3/7	06°35′	162°20′	58
4/25	08°00′	176°00′	67	4/22	07°00′	174°45′	86	3/14	07°20′	161°15′	89
4/26	08°00′	177°00′	119	9/1	13°00′	171°00′	96	3/16	08°10′	165°13′	67
5/8	07°54′	165°32′	118	11/7	16°30′	159°20′	152	3/22	11°32′	168°29′	104
5/8	07°54′	165°32′	113	11/7	16°30′	159°20′	158	3/22	11°32′	168°29′	116
5/8	07°54′	165°32′	104	11/7	16°30′	159°20′	142	3/28	09°10′	153°00′	168
5/8	07°54′	165°32′	113	11/8	16°20′	159°09′	152	5/5	08°13′	175°42′	83
5/8	07°54′	165°32′	88	11/22	17°00′	168°00′	105	5/5	08°13′	175°42′	92
5/8	07°54′	165°32′	106	11/29	17°07′	170°43′	119	5/5	08°13′	175°42′	97
5/8	07°54′	165°32′	125	11/29	17°07′	170°43′	115	5/7	08°00′	175°45′	94
5/10	07°46′	165°29′	121	11/29	17°07′	170°43′	91	5/9	08°28′	175°57′	53
5/10	07°46′	165°29′	88	12/14	17°50′	159°30′	137	6/8	07°15′	164°42′	74
5/19	05°29′	170°06′	48	12/14	17°50′	159°30′	148	6/29	30°49′	166°13′	314
5/19	06°00′	172°00′	47	12/17	16°11′	157°27′	100	7/12	28°50′	156°03′	297
5/23	06°00′	173°00′	58	12/21	17°52′	158°20′	138	7/15	28°05′	155°24′	317
5/26	06°23′	173°59′	99	12/22	10°00′	174°00′	159	7/23	28°44′	154°15′	321
6/1	05°52′	174°41′	48	12/25	18°00′	163°00′	130	7/23	28°44′	154°15′	316
6/1	05°52′	174°41′	73	12/25	18°00′	163°00′	164	7/24	28°22′	154°24′	301
6/20	06°43′	171°26′	53	12/28	17°30′	162°10′	162				
6/25	07°18′	172°53′	86	12/29	12°00′	171°00′	93				
8/18	26°00′	175°00′	357	12/30	12°00′	171°00′	115				
8/21	26°00′	176°00′	358	12/31	12°00′	171°00′	93				
9/4	24°00′	174°00′	328								
9/5	25°00′	174°00′	343								
9/9	25°00′	171°00′	333								
9/9	25°00′	171°00′	301								
9/13	18°00′	170°00′	230								
9/13	18°00′	170°00′	230								
9/13	18°00′	170°00′	223								
9/19	16°00′	173°00′	110								
10/4	09°00′	179°00′	93								
10/4	09°00′	179°00′	116								
10/4	15°00′	173°00′	93								
10/8	19°00′	173°00′	146								
10/9	17°00′	173°00′	185								
10/18	13°00′	174°00′	62								
10/22	15°00′	174°00′	83								
10/22	15°00′	174°00′	93								
10/22	15°00′	174°00′	78								
11/11	16°00′	171°00′	79								
11/13	16°00′	171°00′	62								
11/13	16°00′	171°00′	128								
11/14	16°00′	171°00′	133								
11/15	16°00′	175°00′	150								
11/16	16°00′	172°00′	110								
11/16	16°00′	172°00′	150								
12/18	14°00′	174°00′	102								
12/31	14°00′	175°00′	133								

LENGTH OF JUVENILES

The juvenile albacore in the billfish stomachs ranged from 26 to 358 mm (Figure 1). Two length groups were apparent in the length-frequency distribution: one with a mode at 110 mm and the other at 310 mm; another length group was suggested between 200 and 250 mm.

In the course of the study it became apparent that the larger juveniles were being taken between lat 20° and 30° S. To determine if differences existed in juvenile sizes by latitude, lengths were plotted against latitude of capture (Figure 2). The smallest individuals were taken north of lat 10° S and the largest south of lat 20° S. No specimens smaller than 290 mm were taken south of lat 20° S. The juveniles between lat 10° and 20° S were slightly larger (mean SL 120 mm) than those taken north of lat 10° S (mean SL 94 mm). The mean standard length of those from south of lat 20° S was 324 mm.

In contrast to the latitudinal differences in juvenile length, no longitudinal trends in length were evident. Juveniles larger than 300 mm were taken in the eastern as well as the more westerly portion of the area sampled.

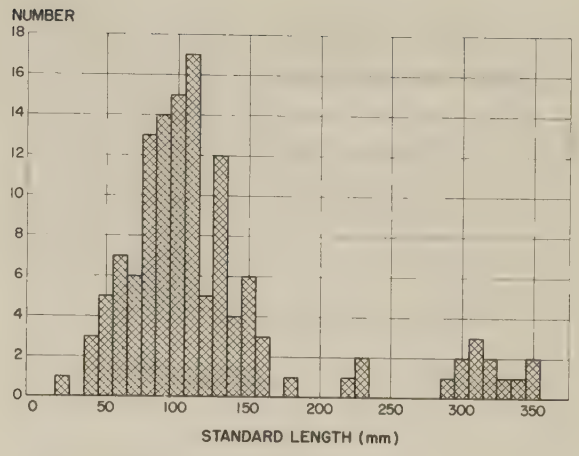

FIGURE 1.—Length-frequency distribution of juvenile albacore in the South Pacific.

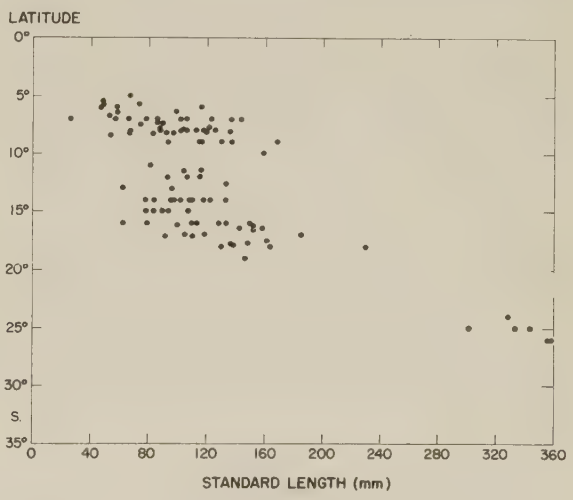

FIGURE 2.—The length of juvenile albacore plotted against latitude of capture.

MIGRATION OF JUVENILES

The differences in the lengths of the albacore in the three latitudinal bands may be caused by the migration of the juveniles. The increase in length of juveniles from north to south and the absence of any longitudinal trends in length suggest a southward migration. After attaining a length of nearly 200 mm the juveniles that originate between the equator and lat 10° S probably start migrating south. They apparently continue to move southward as they grow. This migration would explain the absence of large (>250 mm) juveniles north of lat 20° S.

These observations on the suspected migration pattern of juvenile albacore fit well with the accumulated information on the biology of albacore in the South Pacific. Observations on the length composition of commercial catches of albacore in the South Pacific indicate latitudinal differences in the size of albacore. Adult albacore tend to be small north of lat 15° S and largest between lat 20° and 25° S. They are smaller again south of lat 25° S (Otsu and Sumida, 1968). Length-frequency data published by the Nankai Regional Fisheries Research Laboratory (1959) show that albacore as small as 490 to 500 mm are caught on longlines south of lat 30° S. Thus, it could be that the juveniles move southward as they grow and are first taken by the longline fishery as preadults in the higher latitudes in the South Pacific. A similar pat-

tern has been deduced for albacore in the North Pacific. Otsu and Uchida (1963) hypothesized that the juveniles in the North Pacific migrate from tropical and subtropical waters into temperate waters and are recruited into the adult population in higher latitudes, presumably north of lat 30° N. Generally speaking, then, the albacore in the North and South Pacific, which are believed to constitute separate subpopulations, follow similar migration patterns within their respective hemispheres. The adults are believed to spawn in lower latitudes, between the equator and lat 20° where the eggs hatch and the larvae develop into juveniles. The juveniles then migrate into higher latitudes as they grow and they join the adult population in the higher latitudes.

AGE AND GROWTH

Information on age and growth is useful in determining certain vital statistics for fish populations and it would be useful if the growth of juvenile albacore in the South Pacific could be determined. Around Hawaii juveniles (60-350 mm SL) were estimated to grow about 31 mm per month (Yoshida, 1968). It would have been interesting to compare this growth with that of juveniles in the South Pacific. A plot of juvenile albacore length by time of capture, however, did not indicate that the length of the juveniles was increasing with time.

DISTRIBUTION AND ABUNDANCE

Because the data for any one year were sparse, the data for all years were combined to determine the quarterly distribution of juvenile albacore (Figure 3). The apparent distribution of juvenile albacore may reflect the operations of the longline boats. The longline vessels based at American Samoa primarily were seeking albacore and selecting areas where albacore catch rates tended to be high. The vessels generally fished north of lat 20° S in the first half of the year and beginning in June or July moved southward to as far south as lat 30° S (Otsu and Sumida, 1968). The data indicated that the cooperating vessels generally followed this pattern. In spite of this shortcoming the data suggest some interesting features of the seasonal distribution of juvenile albacore.

In the first quarter billfish stomach samples were collected between long 150° and 178° W and lat 5° and 16° S. The juveniles were generally found throughout the sampling area west of long 153° W.

In the second quarter the longitudinal range of sampling was slightly greater but the juveniles were restricted to the west between long 165° and 179° W. Latitudinally, most of the stomach samples were from north of lat 10° S except for a few samples from about lat 31° S. Juveniles were taken between lat 5° and 9° S and at lat 31° S.

In the third quarter stomach samples were available from long 140° W to 178° E between lat 5° and 31° S. The juveniles were absent in samples from north of 14° S.

In the fourth quarter the sampling area was bounded by long 135° W and 178° E and lat 6° and 21° S. Juveniles were absent from the easternmost portion of the area. They were taken between long 157° and 179° W and lat 9° and 20° S. These observations suggest that the center of the spawning area is closer to the area between long 160° W and the 180th meridian than farther to the east.

Variations were also evident in the apparent abundance of juvenile albacore as indicated by the number of juveniles found monthly per 100 billfish stomachs (Figure 4).

Juvenile albacore were found in all months except July and August. Peaks in apparent abundance occurred in January, April, and November.

The data for all years were pooled because billfish stomachs were unavailable for some months in some years. Also, estimates of apparent abundance may be biased by the small sample sizes. The shortcoming of combining data for all years and considering a large area as an entity is that annual and areal variations in apparent abundance are obscured. For example, in 1965, except in April when four juvenile albacore were taken, no juveniles were found in billfish stomachs from north of lat 10° S.

The overall abundance of juveniles was greater

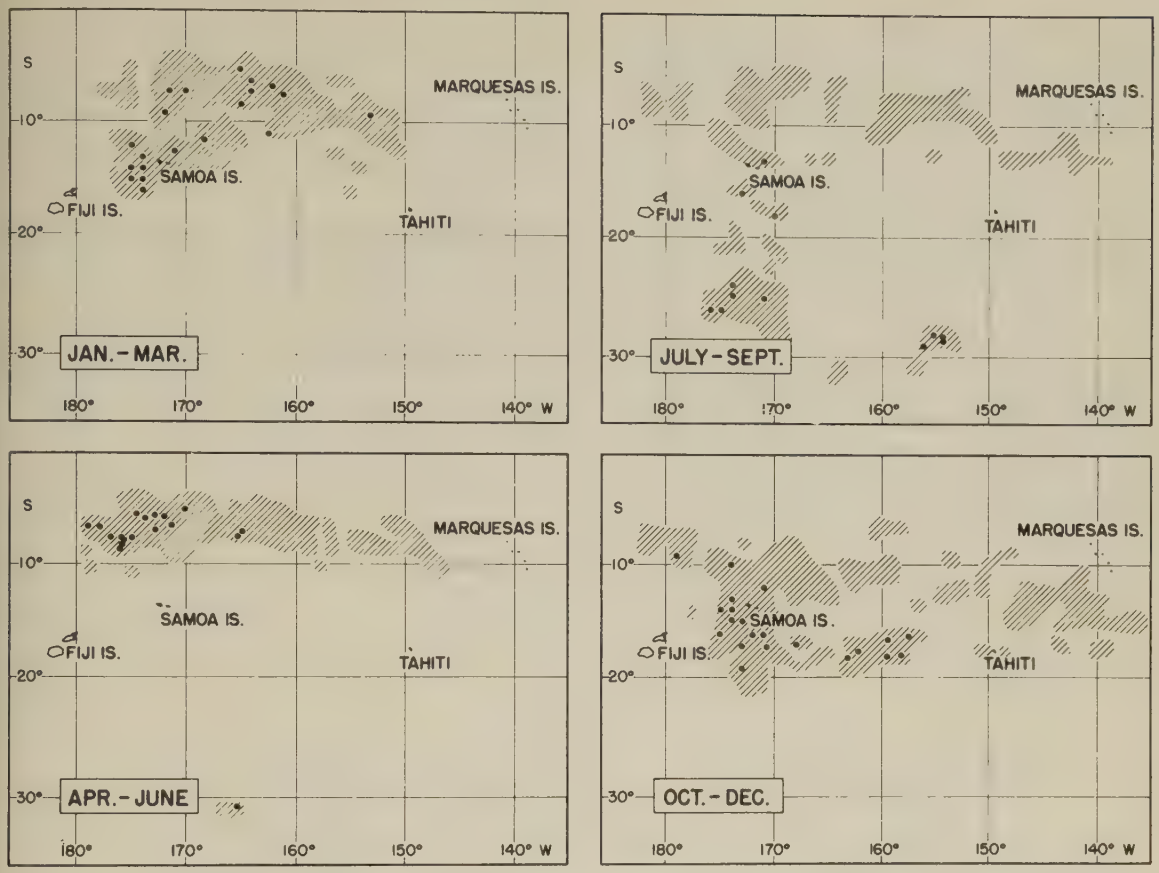

FIGURE 3.—The quarterly distribution of juvenile albacore in the South Pacific, all years combined. The shadings show areas from which billfish stomachs were collected. The dots show where juvenile albacore were taken.

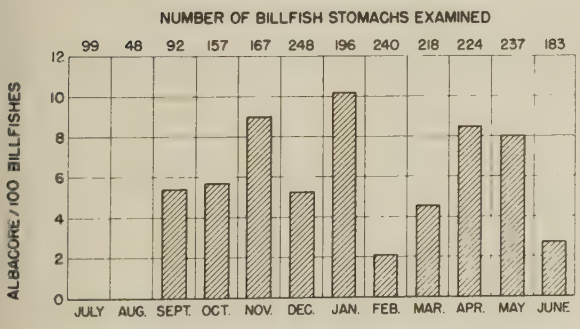

FIGURE 4.—Apparent abundance of juvenile albacore in the South Pacific.

between lat 10° and 20° S than in the area north of lat 10° S. Combining the data for all years, 7.5 juveniles per 100 billfishes were taken between lat 10° and 20° S, and 4.5 juveniles per 100 billfishes were taken north of lat 10° S. (Near Hawaii between July 1962 and April 1966, juvenile albacore were taken at a rate of 0.8 per 100 billfishes [Yoshida, 1968]. Thus, juvenile albacore are apparently more numerous in the South Pacific than around Hawaii.)

SPAWNING

Variations in seasonal and geographic distribution and apparent abundance of juvenile albacore may be related to the spawning of the

adults. Several investigators have made observations on the spawning of albacore in the South Pacific. On the basis of an examination of ovaries, Otsu and Hansen (1962) concluded that peak albacore spawning occurs in the southern hemisphere summer between the equator and lat 20° S. Their results also suggest a spawning season of at least 5 months. Ueyanagi (1969), who based his study on the distribution of larvae and on the stage of maturity of ovaries of adults, also suggested a southern summer spawning season. The seasonal apparent abundance of juvenile albacore does not disagree with the above conclusions. The fact that juveniles were found in all but 2 months of the year suggests a long spawning season. The presence of juvenile albacore during and beyond the southern hemisphere summer indicates some spawning during the summer. My data also suggest annual variations in adult spawning. The virtual absence of juvenile albacore north of lat 10° S in 1965 indicates little or no spawning in this area during that year.

COMPARISON WITH SKIPJACK TUNA

A comparison of the distribution and abundance of juvenile albacore and skipjack tuna offers some interesting contrasts. Although billfish stomachs were sampled from long 135° W to 177° E, juvenile albacore were found only between long 153° and 179° W (Figure 5). The juveniles were found throughout the latitudinal range of sampling between lat 5° and 31° S. Juvenile skipjack tuna are distributed over a wider area: between long 137° W and the 180th meridian from lat 5° to 32° S (Yoshida, 1971). These distributional patterns indicate that skipjack tuna spawn over a wider area than the albacore in the South Pacific.

Comparing the abundance of the two species, in 1964 juvenile skipjack tuna were more numerous north of lat 10° S than from 10° to 20° S, but in 1965 they were more numerous between 10° and 20° S than in the area to the north (Yoshida, 1971). Juvenile albacore were consistently more abundant between lat 10° and 20° S than to the north. Also, juvenile skipjack tuna apparently were from 4.5 to 15 times more numerous than juvenile albacore between the equator and lat 20° S (Table 2). It is also interesting that the apparent abundance of both species declined from 1964 to 1965.

TABLE 2.—Apparent abundance of juvenile albacore and skipjack tuna in the South Pacific. The apparent abundance is expressed as number per 100 billfishes. Data for juvenile skipjack tuna are from Yoshida (1971).

Year	North of lat 10° S		Lat 10°-20° S	
	Albacore	Skipjack tuna	Albacore	Skipjack tuna
1964	6.7	46.3	9.3	42.6
1965	1.9	28.8	5.8	35.6

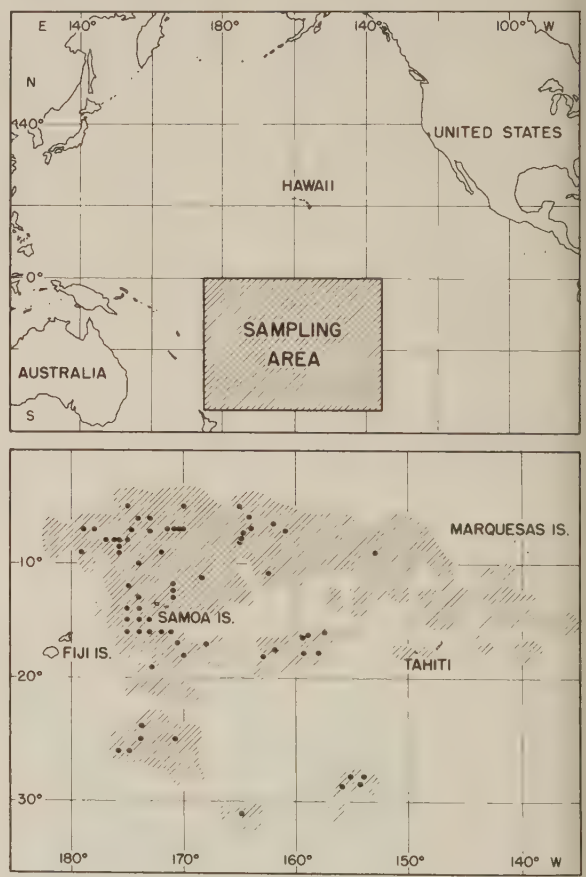

FIGURE 5.—The distribution of billfishes (shading) sampled by the cooperating longline vessels and the distribution of juvenile albacore (dots) found in the billfish stomachs.

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COMPARISON OF PHYTOPLANKTON PRODUCTION BETWEEN NATURAL AND ALTERED AREAS IN WEST BAY, TEXAS[1]

JANE CORLISS AND LEE TRENT[2]

ABSTRACT

Phytoplankton production was compared between an undredged marsh area, a bay area, and an adjacent marsh area altered by channelization, bulkheading, and filling. Average gross production (mg carbon/liter/day) in the altered area (canals) was 8% higher than in the marsh and 48% higher than in the bay during June, July, and August 1969. Gross and net production were significantly higher in the canals and marsh than in the bay; differences between the canals and marsh were not significant.

Large areas of shallow bays and marshes are being dredged, bulkheaded, and filled for waterfront housing sites along the Gulf of Mexico coast. When these sites are developed, shallow marsh and bay areas are deepened or filled with spoil, thus changing the environment for marine organisms. Major changes to the bayshore environment as a result of these alterations include: (1) reduction in acreage of natural shore zone and marsh vegetation; (2) changes in marsh drainage patterns and nutrient inputs; and (3) changes in water depth and substrates. The effects of these environmental changes on the productivity of estuarine organisms are poorly understood.

Basic production in estuaries results from four types of plant life: phytoplankton, attached algae, sea grasses, and emergent vegetation. Production of sea grasses and emergent vegetation is reduced or lost when natural marsh areas are dredged and filled for housing sites. Whether or not this reduction in primary production by sea grasses and emergent vegetation is compensated for by an increase in production by phytoplankton and attached algae is not clear. The objective of this study was to compare phytoplankton production between housing development canals, natural marsh areas, and the open bay in a shallow Texas estuary.

STUDY AREA AND METHODS

The study area in West Bay, Texas, included a natural marsh, an open bay area, and the canals of a waterfront housing development (Figure 1). The developed area, which included about 45 hectares of emergent marsh vegetation, intertidal mud flats, and subtidal water area prior to alteration, was reduced to about 32 hectares of subtidal water by dredging and filling. The water volume (mean low tide level) was increased from about 184,000 to about 394,000 kliter.

Sampling stations were established in dead-end canals in a housing development, natural marsh areas, and an open bay area (Figure 1). Water depths at mean low tide at stations 1 through 5 were 1.6, 2.6, 0.5, 0.2, and 1.0 m respectively.

Primary production was measured on six occasions at each station between June 18 and August 14, 1969. Measurements were made using the light- and dark-bottle technique designed by Gaarder and Gran (1927). Water samples were taken 15 cm below the surface at all stations. A 4-liter bottle having a vent at the bottom with a 30-cm rubber tube attached was used to take the subsurface samples. Number 10 netting (0.060-mm mesh) was placed over the mouth of the bottle and the bottle was submerged, mouth down, until the container filled. The netting was used to eliminate most of the zooplankton from the samples.

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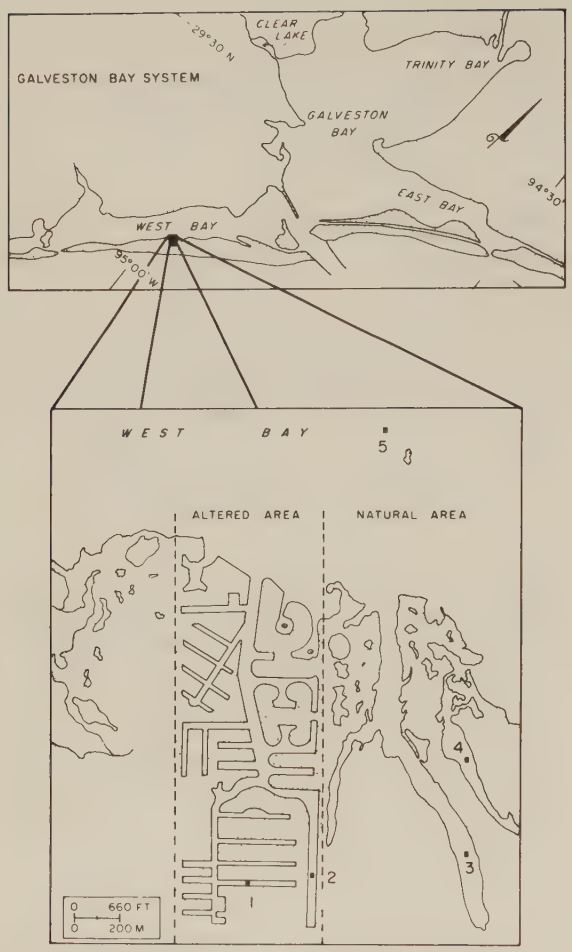

FIGURE 1.—Study area and sampling locations in the Jamaica Beach area of West Bay, Tex.

For each station, six biological oxygen demand (BOD) bottles (300 ml)—two wrapped with black rubber tape and four unwrapped—were filled (gravity flow) from the 4-liter water sample by inserting the rubber tube down to the bottom of each bottle. About 300 ml of water was permitted to overflow after the bottle was full. Two of the unwrapped bottle samples were fixed immediately for oxygen determination. The remaining bottles were stoppered and suspended 15 cm below the surface. The time of sampling was recorded for each station and the bottles were recovered 24 hr later and fixed for oxygen determination.

Water temperature (° C) and turbidity in Jackson turbidity unit—JTU (American Public Health Association, 1962)—observations were made just before the water samples for plankton were taken (Table 1); insolation was measured with a recording pyrheliometer located at station 1.

TABLE 1.—Water temperatures and turbidities observed just before each incubation period.

Date	Station					Average
	1	2	3	4	5	
				°C		
Temperature						
June 18	29.0	29.0	29.0	29.0	29.0	29.0
June 25	31.5	31.0	30.5	30.5	31.0	30.9
July 9	31.5	31.5	31.0	31.0	31.5	31.3
July 24	30.5	29.5	30.0	29.5	29.0	29.7
July 30	32.0	31.0	31.5	31.5	31.0	31.4
Aug. 13	31.5	31.0	30.5	30.5	32.0	31.1
Average	31.0	30.5	30.4	30.0	30.6	30.6
				Jackson turbidity units		
Turbidity						
June 18	9.0	8.0	16.0	16.0	12.0	12.2
June 25	11.5	13.0	29.0	24.5	53.0	26.2
July 9	9.5	8.0	18.0	24.0	14.0	14.7
July 24	12.5	10.0	29.5	24.5	27.0	20.7
July 30	9.0	8.5	21.0	18.5	17.0	14.8
Aug. 13	9.5	6.5	19.0	12.0	18.5	13.1
Average	10.2	9.0	22.1	19.9	23.6	16.9

Dissolved oxygen was measured using a modified Winkler method (Carritt and Carpenter, 1966). Oxygen determinations were made within 3 hr after fixing the water samples. Changes in dissolved oxygen were converted to changes in organic carbon using the relation formulated by Ryther (1956): 1.0 mg oxygen is equivalent to 0.30 mg carbon.

Net production (NP), respiration (R), and gross production (GP) were determined using the carbon values from the initial (I), light (L), and dark (D) bottle values as follows:

$NP = L - I$, $R = I - D$, and $GP = NP + R$.

ENVIRONMENTAL AND HYDROLOGICAL DATA

Surface water temperature varied no more than 1.5° C between stations on any sampling date and no more than 3° C between dates at

any station (Table 1). Surface water temperatures were slightly higher in the canals and bay than in the marsh.

Turbidity values of surface water samples varied as much as 41.5 JTU between stations on June 25 and as much as 41 JTU between dates at station 5 (Table 1). Average turbidity values from the marsh and bay stations were about double those from the canal stations. On June 25, however, turbidities in the bay were about twice those in the marsh and about four times those in the canals.

Insolation was similar on all sampling dates. The daily averages ranged from 0.82 to 0.85 cal/cm^2/day.

Overproduction of phytoplankton, in terms of oxygen balance, occurred in some canals of the development. Plankton blooms that reduced oxygen to zero at night, and caused fish kills at station 1, occurred at least three times during the study period. These blooms were observed on July 4, July 18, and August 7.

PRODUCTION AND RESPIRATION

Average gross production ranged from 1.17 at station 5 to 2.25 mg carbon/liter/day at station 1 during the study (Table 2 and Figure 2). Average values at the two canal stations were almost identical. Likewise, there was almost no difference between average values at the two marsh stations. Average production in the canals was slightly higher (8%) than in the marsh and much higher (48%) than in the bay. In similar studies in Boca Ciega Bay, Fla., Taylor and Saloman (1968) reported that primary production of phytoplankton did not differ consistently between development canals and open bay areas.

Average net production ranged from 0.84 at station 5 to 1.74 mg carbon/liter/day at station 1. Like gross production, the values were about the same among canal stations and among marsh stations. Average net production in the canals was 13% higher than in the marsh and 51% higher than in the Bay.

Respiration averaged 0.51 mg carbon/liter/day, or 27.7% of gross production and ranged from 23.4 to 34.4% between stations (Table 2).

TABLE 2.—Net production (*NP*), respiration (*R*), gross production (*GP*), and percent respiration (*%R*) by station and date in West Bay, Tex.

Date	Variable	Station					Average
		1	2	3	4	5	
		— — — *mg carbon/liter/day* — — —					
June 18	*NP*	2.01	0.91	0.70	1.08	0.54	1.05
	R	0.23	0.69	0.58	0.31	0.34	0.43
	GP	2.24	1.60	1.28	1.39	0.88	1.48
	%R	10.3	43.1	45.3	22.3	38.6	31.9
June 25	*NP*	1.33	1.75	0.87	1.04	0.74	1.15
	R	0.39	1.07	0.63	0.52	0.37	0.60
	GP	1.72	2.82	1.50	1.56	1.11	1.74
	%R	22.7	37.9	42.0	33.3	33.3	33.8
July 9	*NP*	1.80	1.08	1.61	1.34	0.84	1.33
	R	0.37	0.56	0.53	0.43	0.31	0.44
	GP	2.17	1.64	2.14	1.77	1.15	1.77
	%R	17.0	34.1	24.8	24.3	26.9	25.4
July 24	*NP*	2.57	3.04	1.77	2.40	0.94	2.14
	R	0.43	0.38	0.44	0.70	0.32	0.45
	GP	3.00	3.42	2.21	3.10	1.26	2.60
	%R	14.3	11.1	19.9	22.6	25.4	18.7
July 30	*NP*	0.81	1.30	1.82	2.12	0.74	1.36
	R	0.74	0.46	1.19	0.40	0.32	0.62
	GP	1.55	1.76	3.01	2.52	1.06	1.98
	%R	47.7	26.1	39.5	15.9	30.2	31.9
Aug. 13	*NP*	1.94	1.90	1.43	1.57	1.26	1.62
	R	0.87	0.33	0.77	0.44	0.31	0.54
	GP	2.81	2.23	2.20	2.01	1.57	2.16
	%R	30.9	14.8	35.0	21.9	19.7	24.5
Average	*NP*	1.74	1.66	1.37	1.59	0.84	1.44
	R	0.50	0.58	0.69	0.47	0.33	0.51
	GP	2.25	2.24	2.06	2.06	1.17	1.95
	%R	23.8	27.8	34.4	23.4	29.0	27.7

Distinct differences in the percents of gross production attributable to respiration between canal, marsh, and bay areas were not apparent.

Averages of gross and net production in the canals and marsh were significantly greater than in the bay; differences between the canals and marsh were not significant (Table 3).

The differences in production between stations were related to turbidity. The correlation coefficient (r) between average gross production and average turbidity at each station was —0.70.

TABLE 3.—Comparisons of net productivity, respiration, and gross productivity between stations (one-way analysis of variance).

	Comparison between			
	Stations 1-5		Stations 1-4	
	df	*F*-value[1]	df	*F*-value
Net production	4,25	4.06*	3,20	0.72
Respiration	4,25	2.30	3,20	0.97
Gross production	4,25	5.05**	3,20	0.25

[1] Significance level:
* 5%
** 1%

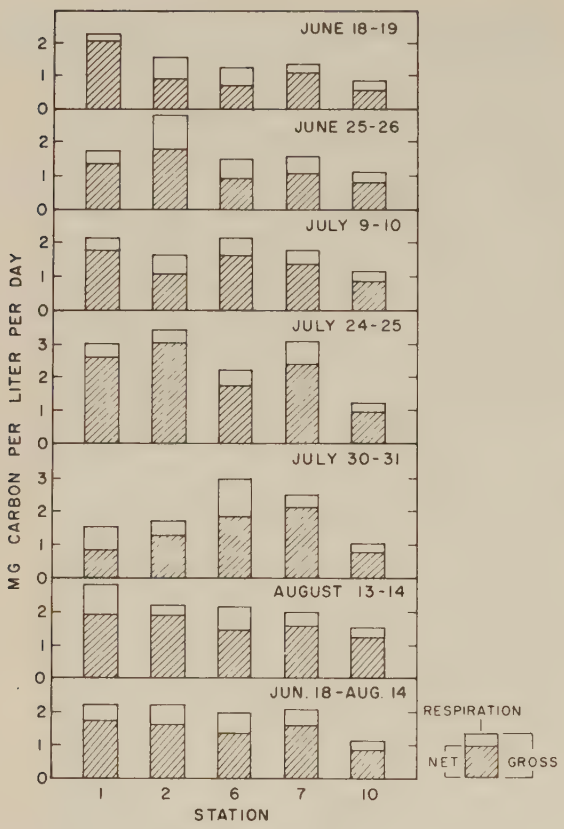

FIGURE 2.—Gross and net production and respiration by station and date, and average values for all sampling dates.

DISCUSSION

It is probable that eutrophic conditions will develop more frequently in housing development canals than in natural marsh areas because of differences in phytoplankton production, water circulation, water exchange, and high nutrient levels. In this study, gross production of phytoplankton in surface waters was higher in the canals than in the marsh or bay. We did not obtain information for computing production per unit area, but it is probable that production per unit area was significantly greater in the canals than in the other two areas, the reasons being the greater depths and lower turbidities in the canals. Wind-driven circulation responsible for reaeration of the waters in the development is less than in the natural area because of houses blocking and diverting prevailing winds and because many of the canals are narrow and perpendicular to the direction of prevailing summer winds. Water depths at mean low tide in the development averaged about 1.5 m but were often much greater, sometimes over 3 m, whereas depths in the natural area averaged about 0.6 m but were always less than 1 m. With the average tide level change of 0.3 m, this means that only about one-fifth of the volume of water in the development exchanges with the bay during a normal tidal cycle, whereas about one-half exchanges per cycle in the natural area. Nutrient levels were about the same (nitrogen) or slightly higher (phosphates) in the canals than in the natural area (Moore and Trent, 1971). It is possible, however, that because of reduced water exchange, nutrient levels in parts of the development were too high to maintain a balanced ecological system.

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THERMAL TOLERANCE OF JUVENILE PACIFIC SALMON AND STEELHEAD TROUT IN RELATION TO SUPERSATURATION OF NITROGEN GAS

WESLEY J. EBEL, EARL M. DAWLEY, AND BRUCE H. MONK[1]

ABSTRACT

Thermal tolerance of juvenile chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), and steelhead trout (*Salmo gairdneri*) that had been held at various acclimation temperatures was lowered when test water was supersaturated (125-130% of saturation) with nitrogen gas. Increasing the depth of the test tank allowed the fish to compensate somewhat for the supersaturation by sounding, but substantial mortalities still occurred. A comparison of tolerance among the species tested revealed that coho salmon were the most tolerant, chinook salmon next, and steelhead trout the least tolerant to temperature increases in the presence of supersaturation of nitrogen.

During the past several decades, a number of investigators have examined temperature as a lethal factor by use of the classic pharmacological assay method. Fry, Hart, and Walker (1946) recognized the importance of acclimation temperature in determining the tolerance of a fish to high and low temperatures and established upper and lower levels of tolerance at various acclimation temperatures. Brett (1952) listed maximum temperatures for survival of young Pacific salmon (*Oncorhynchus* spp.) between 23.8 and 25.1° C. In later work (Brett, 1958), he emphasized temperatures below those at which a fish dies and constructed hypothetical temperature polygons which described lower levels of temperature tolerance where activity, growth, and spawning would be affected.

More recently, investigators have emphasized the response of fish to temperature changes under multivariate conditions. Many factors such as dissolved oxygen deficits, carbon dioxide increases, and increases in toxic substances all affect an aquatic organism's tolerance to temperature increases. Mihursky and Kennedy (1967) stressed the importance of multivariate experiments for establishing more realistic standards for temperature regulation.

Several nuclear power plants have been proposed for the Columbia River. The National Marine Fisheries Service (NMFS) is particularly concerned about the effect that heated effluents from these plants might have on juvenile Pacific salmon and steelhead trout (*Salmo gairdneri*) migrating downstream, particularly while they are stressed by supersaturated nitrogen gas. High levels of nitrogen gas (over 125% saturation) occur within large areas of the Columbia from about early May until mid-August (Ebel, 1969). This period coincides with the downstream migration of most juvenile salmon and trout. Although the effect of supersaturation of gas on juvenile salmon and trout has not been examined in great detail, preliminary studies by Ebel (1969) clearly show that Columbia River juvenile salmon have considerably lower tolerance to temperature increases when stressed by supersaturation of nitrogen than the tolerance indicated by Brett (1952).

The Federal Water Quality Administration (FWQA) recognized that supersaturation of dissolved nitrogen could be a significant factor in establishing water quality criteria for the Columbia River. It therefore contracted the Bureau of Commercial Fisheries (BCF; presently designated as NMFS) to determine the changes in tolerance of juvenile salmon and trout to temperature increases at different levels

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of temperature acclimation and supersaturation of nitrogen. In the experiments described in this report, BCF personnel sought to determine the change in tolerance of juvenile salmon and trout to temperature increases when stressed by supersaturation of nitrogen and to determine possible changes in tolerance if they had the option to sound to different depths. Ebel (1969) reported that the depth at which fish migrate influences the effect of supersaturation of nitrogen because the gas remains in solution at a much higher concentration when under pressure; we therefore considered depth as well as temperature increase and supersaturation of nitrogen to be important.

Our first series of experiments describe the effect of supersaturation of nitrogen and temperature increases at surface pressures. Later experiments show how depth changes the above effect.

METHODS

The general approach used to determine the effect of nitrogen supersaturation on the tolerance of juvenile salmon and trout to increased temperature was similar to that used by Brett (1952). Stocks were acclimated to temperatures identical to those used by Brett; test temperatures encompassed the ranges Brett used in his lethal temperature determinations. These test and acclimation temperatures were purposely selected so that changes in tolerance caused by the stress of supersaturated nitrogen could be compared with Brett's well-established levels of temperature tolerance.

Groups of 20 test fish, each acclimated to a given temperature, were placed simultaneously in control and test situations involving identical test temperatures at treatments of high (125-130%) and normal (100%) nitrogen saturation. Two acclimation groups were used in each set of tests—one that had a normal acclimation history and one that had been exposed to supersaturated nitrogen for 720 min. Observations of behavior and mortality were made continuously for the first 6 hr, then every hour for the remainder of an 18-hr period. Events recorded were times to first indication of stress, to loss of equilibrium, and to death. The numbers of live and dead fish with obvious external symptoms of gas bubble disease were recorded at the termination of tests. All tests were then repeated (most tests were duplicated, some were done three times); the data given in this report are derived from the average value of the duplicated tests.

Hatchery and wild stocks of fish were tested. Hatchery fish were from the following stocks: coho salmon (*O. kisutch*) reared at Leavenworth National Fish Hatchery, Leavenworth, Wash.; spring chinook salmon (*O. tshawytscha*) reared at Little White Salmon National Fish Hatchery, White Salmon, Wash.; and steelhead trout reared at the Washington State Fish Hatchery at Green River, Cumberland, Wash. The wild fish (spring chinook salmon) were collected from the turbine intake gatewells at McNary Dam on the Columbia River. Because of time limitations and lack of sufficient populations of fish, only the coho were tested through the entire range of acclimation temperatures (5, 10, 15, and 20° C). Hatchery-reared steelhead trout and hatchery and wild spring chinook were tested only after exposure at selected acclimation temperatures—steelhead at acclimation temperatures of 10° and 15° C and wild chinook at 10° C.

The experimental temperatures (test and acclimation), lengths of time that the various groups of fish were in holding and acclimation tanks, and size of fish at time of testing are summarized in Table 1. Water in test tanks was adjusted to the appropriate test temperatures established for each acclimation temperature. Temperatures were maintained within ±0.2° C in both test and acclimation tanks. When the test series required stressing of the acclimated fish with supersaturated nitrogen, an acclimation tank at the appropriate temperature was saturated at 115 to 120% nitrogen and about 114 to 120% oxygen. The fish were then transferred from the normally saturated tank (100%) to the supersaturated tank and stressed for 720 min. When supersaturated water was needed in the test tanks, the supersaturating equipment was activated, and each tank was adjusted to maintain between 125 and 130% nitrogen. To ensure stability, the temperatures and satura-

TABLE 1.—Holding time and temperature of water before transfer to acclimation tanks, acclimation conditions, and mean size at time of testing of three species of salmon and trout.

Species and origin of fish	Time in holding tank	Water temperature in holding tank	Acclimation conditions		Mean size of fish at time of test	
			Days	Temperature	Length	Weight
	days	*° C*		*° C*	*mm*	*g*
Hatchery coho	28	8.8	35	5.0a	117	17
	28	8.8	17	10.0a	118	18
	28	8.8	23	10.0	134	22
	28	8.8	4	12.5	134	22
	28	8.8	48	15.0a	134	22
	28	8.8	3	11.7	118	18
	28	8.8	4	14.0	118	18
	28	8.8	16	15.0	118	18
	28	8.8	4	17.5	118	18
	28	8.8	3	20.0a	118	18
Wild spring chinook	0	15.0	4	10.0a	129	19
Hatchery spring chinook	90	8.8-13.0	4	15.0a	134	23
	90	8.8-13.0	3	15.0	134	23
	90	8.8-13.0	3	17.0	134	23
	90	8.8-13.0	3	20.0a	134	23
Hatchery steelhead	10	12.0	5	10.0a	179	54
	10	12.0	3	14.0	179	54
	10	12.0	42	15.0a	179	54

a Final acclimation temperature.

tion levels were then measured for 24 hr before introduction of the test fish.

The source of supersaturation of nitrogen gas in the Columbia River was entrained air. We used pumps to entrain air in our test and acclimation tanks. Oxygen, therefore, was also supersaturated; the ratio of oxygen to nitrogen supersaturation was similar to that recorded in the river (Beiningen and Ebel, 1971). Oxygen saturation varied from about 114 to 120%.

Facilities used for tolerance tests in relation to supersaturation of nitrogen at surface pressures were designed to provide a continuous supply of fresh water. Sufficient cooling and heating capacity was available from a water heater and chiller to continuously supply 227 liters/min of either heated or chilled water from 5° to 40° C. Ten cylindrical fiber glass acclimation tanks, about 1 m high × 2½ m in diameter, provided sufficient space to maintain 2000 fish at each of five acclimation temperatures without crowding. The test tanks were rectangular fiber glass tanks of 113.6-liter capacity. A flow of approximately 11.5 to 30.0 liters/min was maintained in acclimation tanks and 3.5 liters/min in test tanks.

Supersaturation of nitrogen and oxygen was achieved in the acclimation tanks by metering air into the intake of two high-pressure recirculating pumps with 42 kg/cm² back pressure on the discharge side of the pump. About 0.75 liter/min air in each pump created the desired saturation of nitrogen (115-120%). Supersaturation of nitrogen and oxygen in the test tanks was achieved by metering 0.05 liter/min into another high-pressure recirculating pump with 32 kg/cm² back pressure, which recirculated the water in the coldwater supply tank to the test tanks. (Source of water was from Seattle municipal supply; chlorine was eliminated by charcoal filters.) The final saturation value for each tank was then achieved by manipulating the number of equilibrating screens through which the water flowed before entering the tanks.

The test tank (9 m deep) used for our experiments concerning water depth has been described by Pugh, Groves, and Ebel (1969). When tolerance tests were conducted in the deep tank, the saturation levels of nitrogen and oxygen were controlled in the above manner (by injecting air into a recirculating pump). Because of the large volume of water (66,648 liters), a continuous flow of fresh water was not needed and the existing water was recirculated. Time limitations precluded testing more than two populations (hatchery coho and wild spring

chinook salmon) at 10° C acclimation temperature.

EFFECT OF SUPERSATURATION OF NITROGEN GAS ON TOLERANCE OF FISH TO TEMPERATURE INCREASES

Supersaturation of nitrogen (125-130%) in the test tanks lowered the tolerance of all fish to temperature increases at all acclimation temperatures when tested below 26° C (Tables 2-10). More than 50% mortality occurred within 18 hr even with no temperature increase when the test tanks were supersaturated at this level. Time to death of fish was accelerated regardless of acclimation temperature.

A comparison of LE_{50} (exposure time when 50% of the population is dead) curves developed under the four treatment levels indicates that a prior stress of 115 to 120% saturation for 12 hr did not greatly affect the fish when they were subjected to temperature increases in water saturated at 100% (Figure 1). When these

TABLE 3.—Mean values[a] of lethal exposure time (in minutes) for coho salmon that had been acclimated to 10° C water temperature and then subjected to various increases in water temperature and saturation of nitrogen gas.

Dead fish in sample	Level of gas[b]	Lethal exposure time at various temperatures (° C)					
		10	15	20	23	25	27
One fish	NN	--	--	--	--	130	4
	NS	773	413	360	215	130	6
	SN	--	--	--	--	135	4
	SS	770	407	340	155	125	12
Three fish	NN	--	--	--	--	100	< 5
	NS	877	472	517	297	152	16
	SN	--	--	--	--	67	7.5
	SS	960	480	382	225	95	15
Half of sample	NN	--	--	--	--	167	15
	NS	--	1,085	540	550	192	23
	SN	--	--	--	--	232.5	16.5
	SS	960	480	480	282.5	193.5	35.5
All of sample	NN	--	--	--	--	215	32.5
	NS	--	--	--	--	255	72.5
	SN	--	--	--	--	255	35
	SS	--	--	1,050	750	395	70

a Mean of replicated tests.
b NN = normal saturation (100%) of nitrogen gas in acclimation and test tanks;
NS = normal saturation in acclimation tank and supersaturation (125-130%) in test tanks;
SN = supersaturation in acclimation tank and normal saturation in test tanks;
SS = supersaturation in acclimation and test tanks.

TABLE 2.—Mean values[a] of lethal exposure time (in minutes) for coho salmon that had been acclimated to 5° C water temperature and then subjected to various increases in water temperature and saturation of nitrogen gas.

Dead fish in sample	Level of gas[b]	Lethal exposure time at various temperatures (° C)					
		5	10	15	20	23	25
One fish	NN	--	--	--	--	125	15.5
	NS	525	412	380	230	85	14
	SN	--	--	--	--	102	8
	SS	250	330	197	112	35	10
Three fish	NN	--	--	--	--	167	20.5
	NS	615	457	405	270	108	16.5
	SN	--	--	--	--	270	12
	SS	483	435	315	128	137	13
Half of sample	NN	--	--	--	--	300	27
	NS	810	605	577	390	266	21.5
	SN	--	--	--	--	--	20
	SS	626	580	435	229	186	20
All of sample	NN	--	--	--	--	--	64
	NS	--	990	--	1,080	420	58
	SN	--	--	--	--	--	60
	SS	--	--	--	840	450	445

a Mean of replicated tests.
b NN = normal saturation (100%) of nitrogen gas in acclimation and test tanks;
NS = normal saturation in acclimation tank and supersaturation (125-130%) in test tanks;
SN = supersaturation in acclimation tank and normal saturation in test tanks;
SS = supersaturation in acclimation and test tanks.

TABLE 4.—Mean values[a] of lethal exposure time (in minutes) for coho salmon that had been acclimated to 15° C water temperature and then subjected to various increases in water temperature and saturation of nitrogen gas.

Dead fish in sample	Level of gas[b]	Lethal exposure time at various temperatures (° C)					
		15	20	23	26	27	28
One fish	NN	--	--	--	--	26.5	8.5
	NS	420	265	2,325	222.5	38.5	7
	SN	--	--	--	255	23	10
	SS	70	36	45	29.5	17.5	12.5
Three fish	NN	--	--	--	--	50	10.5
	NS	430	295	297	245	51.5	14
	SN	--	--	--	705	30	14
	SS	175.5	78.5	62.5	38.5	32.5	18
Half of sample	NN	--	--	--	--	62	13.5
	NS	555	502.5	517.5	645	79	20.5
	SN	--	--	--	855	70	24.5
	SS	247	115	124.5	86	52.5	38
All of sample	NN	--	--	--	--	93	37
	NS	--	--	--	--	115	46
	SN	460	520	930	910	115	48
	SS	519	450	465	312.5	96	38

a Mean of replicated tests.
b NN = normal saturation (100%) of nitrogen gas in acclimation and test tanks;
NS = normal saturation in acclimation tank and supersaturation (125-130%) in test tanks;
SN = supersaturation in acclimation tank and normal saturation in test tanks;
SS = supersaturation in acclimation and test tanks.

TABLE 5.—Mean values[a] of lethal exposure time (in minutes) for coho salmon that had been acclimated to 20° C water temperature and then subjected to various increases in water temperature and saturation of nitrogen gas.

Dead fish in sample	Level of gas[b]	Lethal exposure time at various temperatures (° C)					
		20	23	25	27	28	29
One fish	NN	--	--	--	93	35	14
	NS	375	558	400	130	29	11
	SN	130	--	15	47	17	7.5
	SS	89	20	135	45	13	9.5
Three fish	NN	--	--	--	104	47	14
	NS	497	510	510	152	38	13
	SN	--	--	--	82	34	13
	SS	180	300	165	69	30	12
Half of sample	NN	--	--	--	121.5	60	20
	NS	810	780	840	197	43	20
	SN	--	--	--	115	53.5	22
	SS	317.5	570	266	115	42.5	16
All of sample	NN	--	--	--	--	93.5	37
	NS	920	1,040	930	910	115	48
	SN	--	--	--	--	115	46
	SS	619	450	465	307	97	38.5

a Mean of replicated tests.
b NN = normal saturation (100%) of nitrogen gas in acclimation and test tanks;
NS = normal saturation in acclimation tank and supersaturation (125-130%) in test tanks;
SN = supersaturation in acclimation tank and normal saturation in test tanks;
SS = supersaturation in acclimation and test tanks.

TABLE 6.—Mean values[a] of lethal exposure time (in minutes) for hatchery spring chinook salmon that had been acclimated to 15° C water temperature and then subjected to various increases in water temperature and saturation of nitrogen gas.

Dead fish in sample	Level of gas[b]	Lethal exposure time at various temperatures (° C)					
		15	20	23	25	27	28
One fish	NN	--	--	--	90.5	22	5
	NS	510	585	375	210	16.5	4.5
	SN	450	--	390	30	75	4
	SS	32.5	30	30	20.5	6.5	3
Three fish	NN	--	--	--	255	55	9
	NS	510	735	510	198	45	8.5
	SN	--	--	--	245	9	6.5
	SS	217	190	110	80	11	4
Half of sample	NN	--	--	--	360	66	115
	NS	675	820	540	255	52.5	10.5
	SN	--	--	--	370	39.5	9
	SS	315	165	123	122.5	16.5	6
All of sample	NN	--	--	--	1,020	88.5	30.5
	NS	900	1,080	755	275	97	25
	SN	--	--	--	700	78.5	19.5
	SS	720	780	525	399	50	40.5

a Mean of replicated tests.
b NN = normal saturation (100%) of nitrogen gas in acclimation and test tanks;
NS = normal saturation in acclimation tank and supersaturation (125-130%) in test tanks;
SN = supersaturation in acclimation tank and normal saturation in test tanks;
SS = supersaturation in acclimation and test tanks.

TABLE 7.—Mean values[a] of lethal exposure time (in minutes) for hatchery spring chinook salmon that had been acclimated to 20° C water temperature and then subjected to various increases in water temperature and saturation of nitrogen gas.

Dead fish in sample	Level of gas[b]	Lethal exposure time at various temperatures (° C)					
		20	23	25	27	28	29
One fish	NN	--	--	720	34	33.5	5
	NS	255	150	--	71.5	38.5	9.5
	SN	--	--	41.5	6	8.5	5.5
	SS	30	30	7.5	15	10.5	3
Three fish	NN	--	--	--	84.5	44.5	6.5
	NS	360	345	372	86	43.5	14.5
	SN	--	--	795	39.5	16	7.5
	SS	45	67.5	30	28	16.5	4.5
Half of sample	NN	--	--	--	95	51.5	8
	NS	450	435	570	97	48.5	17
	SN	--	--	620	66	23	8.5
	SS	75	176	42.5	44	22	6.5
All of sample	NN	--	--	--	153.5	63.5	13.5
	NS	780	690	750	133	66	27.5
	SN	--	--	820	110	46.5	19
	SS	397	675	600	97.5	52.5	13.5

a Mean of replicated tests.
b NN = normal saturation (100%) of nitrogen gas in acclimation and test tanks;
NS = normal saturation in acclimation tank and supersaturation (125-130%) in test tanks;
SN = supersaturation in acclimation tank and normal saturation in test tanks;
SS = supersaturation in acclimation and test tanks.

TABLE 8.—Mean values[a] of lethal exposure time (in minutes) for wild spring chinook salmon that had been acclimated to 10° C water temperature and then subjected to various increases in water temperature and saturation of nitrogen gas.

Dead fish in sample	Level of gas[b]	Lethal exposure time at various temperatures (° C)					
		10	15	20	23	25	27
One fish	NN	--	--	61	118	9	4
	NS	600	645	463	163	17	3
	SN	--	98	312	4	2	1
	SS	38	35	68	10	3	1
Three fish	NN	--	--	--	--	192.5	27
	NS	--	--	--	720	465	43
	SN	--	--	--	--	80	9
	SS	660	660	600	780	71.5	6
Half of sample	NN	--	--	--	--	82.5	5
	NS	--	--	780	405	195	4
	SN	--	--	--	1,080	7.5	2
	SS	495	187	150	58	7.5	3
All of sample	NN	--	--	--	--	193	27
	NS	--	--	--	900	165	43
	SN	--	--	--	--	80	9
	SS	870	660	600	780	71	6

a Mean of replicated tests.
b NN = normal saturation (100%) of nitrogen gas in acclimation and test tanks;
NS = normal saturation in acclimation tank and supersaturation (125-130%) in test tanks;
SN = supersaturation in acclimation tank and normal saturation in test tanks;
SS = supersaturation in acclimation and test tanks.

TABLE 9.—Mean values[a] of lethal exposure time (in minutes) for steelhead trout that had been acclimated to 10° C water temperature and then subjected to various increases in water temperature and saturation of nitrogen gas.

Dead fish in sample	Level of gas[b]	Lethal exposure time at various temperatures (° C)					
		10	15	20	23	25	27
One fish	NN	--	--	930	458	60	4.5
	NS	195	172.5	230	230	60	8.5
	SN	--	360	--	10	6	6
	SS	57.5	15	6	6	8.5	5.5
Three fish	NN	--	--	--	--	200	10
	NS	280	217	367	320	112	15
	SN	--	--	--	--	206	9
	SS	76	50	71	52	19	11
Half of sample	NN	--	--	--	--	225	14
	NS	307	340	493	450	165	17
	SN	--	--	--	--	366	14
	SS	104	75	105	74	38	15
All of sample	NN	--	--	--	--	675	34
	NS	660	660	780	690	465	80
	SN	--	--	--	--	--	52.5
	SS	347.5	307.5	202.5	202.5	95	30

a Mean of replicated tests.
b NN = normal saturation (100%) of nitrogen gas in acclimation and test tanks;
NS = normal saturation in acclimation tank and supersaturation (125-130%) in test tanks;
SN = supersaturation in acclimation tank and normal saturation in test tanks;
SS = supersaturation in acclimation and test tanks.

TABLE 10.—Mean values[a] of lethal exposure time (in minutes) for steelhead trout that had been acclimated to 15° C water temperature and then subjected to various increases in water temperature and saturation of nitrogen gas.

Dead fish in sample	Level of gas[b]	Lethal exposure time at various temperatures (° C)					
		15	20	23	26	27	28
One fish	NN	--	--	--	225	23	18
	NS	570	480	480	207	37.5	15
	SN	--	--	--	7	9.5	6
	SS	15	25	14	14	8	4.5
Three fish	NN	--	--	--	660	62.5	21
	NS	645	570	600	390	53.5	20
	SN	--	--	--	151.5	16.5	11.5
	SS	30	56	30	21.5	14	11
Half of sample	NN	--	--	--	--	75	24
	NS	840	630	645	435	58	23.5
	SN	--	--	--	495	23.5	15
	SS	45	94	52.5	43	19	19
All of sample	NN	--	--	--	--	107.5	42
	NS	1,320	870	900	720	81.5	34.5
	SN	--	--	--	840	127.5	32.5
	SS	690	452.5	157.5	225	57.2	24.5

a Mean of replicated tests.
b NN = normal saturation (100%) of nitrogen gas in acclimation and test tanks;
NS = normal saturation in acclimation tank and supersaturation (125-130%) in test tanks;
SN = supersaturation in acclimation tank and normal saturation in test tanks;
SS = supersaturation in acclimation and test tanks.

stressed fish were subjected to temperature increases in water supersaturated at 125 to 130%, however, the prior stress significantly decreased their tolerance at temperatures below 26° C. Figure 1 shows only the data from populations acclimated to 15° C (Tables 3, 6, and 10), but similar curves that clearly show the effect of supersaturation can be constructed from the data on populations acclimated to the other temperatures.

Populations of coho salmon, steelhead trout, and chinook salmon acclimated to higher temperatures were able to tolerate higher temperatures for longer periods in supersaturated water as well as in normally saturated water. A comparison of our LE_{50} curves for coho with those of Brett (1952) indicates that tolerance to higher temperatures in supersaturated water

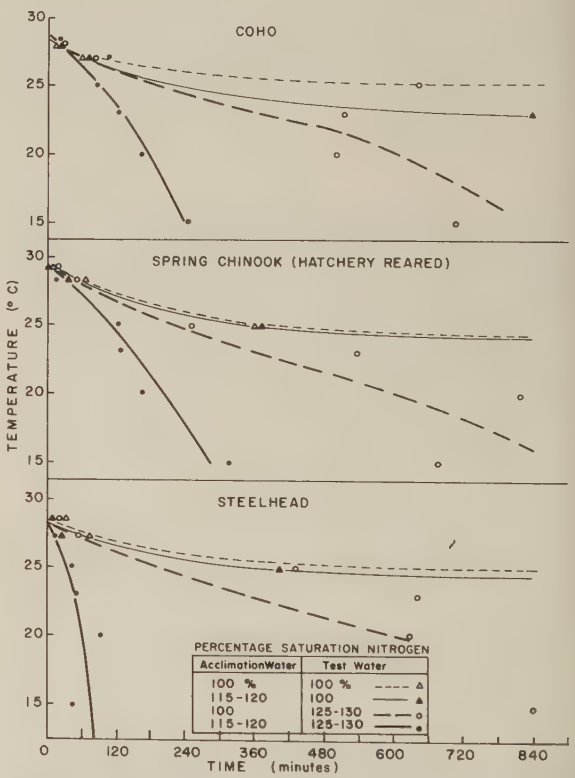

FIGURE 1.—Comparison of LE_{50} curves of hatchery-reared juvenile coho salmon, spring chinook salmon, and steelhead trout acclimated at 15° C and stressed at various levels of nitrogen saturation.

was considerably lower at exposures over 100 min for the same acclimation temperature than at normal saturation levels (Figure 2).

A comparison of the NN and SN curves (Figure 1) indicates that the prior stress of supersaturation of nitrogen had little effect on the fish when they were subjected to test water that was not supersaturated. This suggests that migrating salmon and trout under stress from supersaturation of nitrogen gas could recover from the effects of supersaturation if there were river areas where water would equilibrate. These data also show that salmon and trout populations acclimated at 15° C and subjected to nitrogen saturation of 125 to 130% will probably have about 50% mortality in less than 360 min with no temperature increase when stressed for 12 hr before testing and that subjecting the populations to temperature increases merely reduces the time to death.

In comparing the tolerance to temperature increases between coho and spring chinook salmon, we found that the results from the control tests—where both acclimation and test water were at 100% saturation—were similar to the results of Brett (1952). That is, coho were more tolerant than chinook and the respective upper lethal temperatures were 25 to 26° C. Brett did not study steelhead trout. We found that steelhead trout were nearly identical to coho in their tolerance to temperature increases when supersaturation of nitrogen was not present (control tests) but were the most vulnerable species when supersaturation was entered as a factor. Figure 3 compares the tolerance of three species to temperature increases when acclimation water and test water were supersaturated. Coho were the most tolerant, wild spring chinook next, and steelhead the least tolerant.

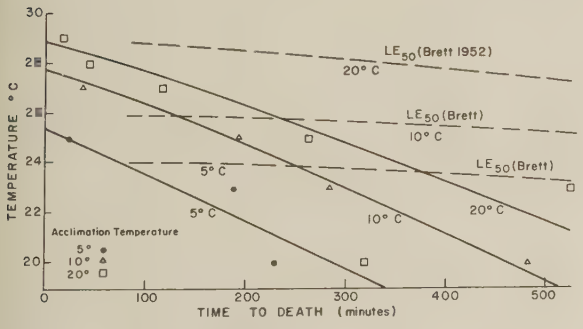

FIGURE 2.—Median-resistance-time (LE_{50}) plotted from temperature tolerance tests with coho salmon fingerlings acclimated at 5°, 10°, and 20° C and stressed for 12 hr at 115-120% saturation of N_2, then subjected to temperature increases in water supersaturated at 125-130%. Brett's LE_{50} curves for fish acclimated at 5° and 20° C—without N_2 stress—are shown for comparison.

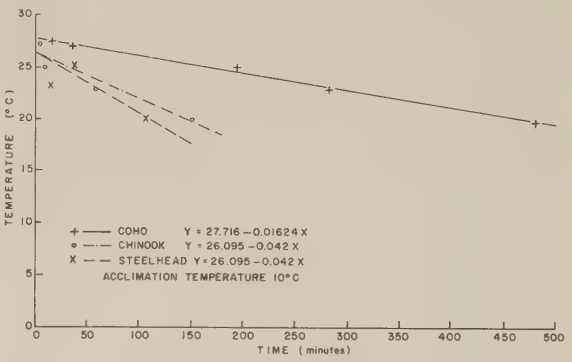
TEMPERATURE (°C)
TIME (minutes)
COHO Y = 27.716 – 0.01624 X
CHINOOK Y = 26.095 – 0.042 X
STEELHEAD Y = 26.095 – 0.042 X
ACCLIMATION TEMPERATURE 10°C

FIGURE 3.—Comparison of LE_{50} values between species of salmonid juveniles (acclimated at 10° C) in tolerance to temperature increases when stressed by 115-120% saturation of nitrogen gas for 12 hr, then subjected to temperature increases in supersaturated water at 125-130% nitrogen.

Size of fish at time of testing could influence the comparison between species. Coho and wild spring chinook acclimated at 10° C were nearly the same size at time of testing (Table 1), but steelhead acclimated at 10° C were larger than the other species when tested. There is evidence that extremely small chinook fry are more susceptible to nitrogen supersaturation than fingerlings; then, as the fingerlings increase in size, they become more susceptible than the small fingerlings but less susceptible than the fry (Meekin, 1969).[2] If this occurs with steelhead also, it could account for their lower tolerance. During one test with coho acclimated at 15° C, we found no differences in susceptibility within the size range tested (101-151 mm) at 125 to 130% saturation.

[2] Personal communication, Thomas Meekin, Washington State Department of Fisheries. Experiments at Priest Rapids Dam.

We intended to compare hatchery-reared chinook salmon with wild or naturally migrating spring chinook salmon acclimated to the same temperature. Wild fish were available only when they were acclimated to temperatures near 10° C. The hatchery population had deteriorated by then, however, so we compared wild fish acclimated at 10° C and hatchery fish acclimated to 15° C (Figure 4). As expected, the hatchery population—acclimated at the higher temperature—was able to tolerate the highest temperatures for a longer period, but when the LE_{50} curves—which include the effect of nitrogen—are compared, little difference can be noted. This indicates that results achieved in the laboratory with hatchery stocks can be applied to wild Columbia River stocks with reasonable accuracy.

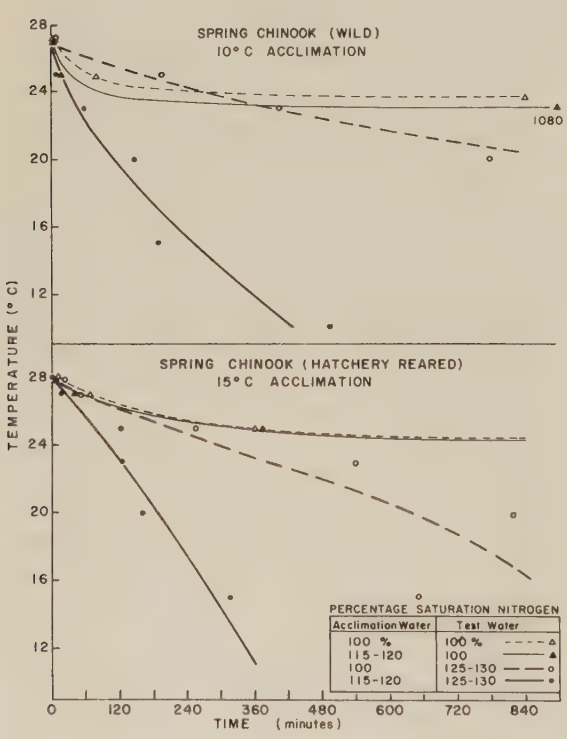

FIGURE 4.—Comparison of LE_{50} curves between juvenile wild and hatchery spring chinook salmon at various temperatures and levels of saturation of nitrogen gas.

EFFECT OF DEPTH ON RELATION BETWEEN SUPERSATURATION OF NITROGEN AND TOLERANCE OF JUVENILE FISH TO TEMPERATURE INCREASES

Examination of fish in cages at the forebay of Priest Rapids Dam (Ebel, 1969) indicated that juvenile coho and chinook salmon would not contract gas bubble disease if held at a sufficient compensating depth (5 m). This finding suggests that fish subjected to temperature increases in addition to nitrogen supersaturation would also be less affected if they remained at sufficient depth when they encountered a temperature increase.

To test this hypothesis, we subjected coho salmon acclimated at 10° C to three temperatures above acclimation in water supersaturated at 130% in the 9-m (deep) tank where they could select any depth from the surface to 9 m; we then compared LE_{100} curves in the 20-cm (shallow) tanks with those in the deep tank (Figure 5). These curves definitely indicate that the coho benefited by having the option to sound in the deep tank. The LE_{100} level never was reached during the 18-hr observation period when the fish were subjected to 20° C (10° C increase) in the deep tank, but occurred after

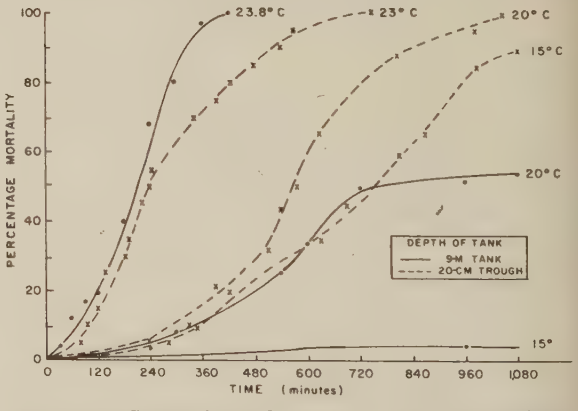

FIGURE 5.—Comparison of LE_{100} curves for coho salmon acclimated at 10° C and subjected to three temperatures (15°, 20°, and 23° C) in 20-cm and 9-m deep tanks containing water supersaturated with nitrogen gas at 130% saturation. Oxygen concentrations varied from 115 to 125% saturation.

about 17 hr in the shallow tank. Similarly at 15° C (5° C increase), the LE_{50} level was never reached in the deep tank but was reached in about 12.5 hr in the shallow tank. No benefit from depth is indicated in the curves at 23° C; in this comparison, the fact that temperature in the deep tank was 0.8° C higher (23.8° C) than that in the shallow tank could account for the lack of difference.

Wild juvenile spring chinook salmon from the gatewells at McNary Dam also were tested in the deep and shallow tanks. These fish were acclimated at 10° C and then subjected to a 5° C increase (15° C) with supersaturation of nitrogen gas at 130% saturation. The fish also were stressed for 12 hr before the test in 10° C water supersaturated at 120% saturation. Again, chinook tested in the deep tank survived at a higher rate than those in the shallow tanks; the LE_{50} was never reached in the deep tank, whereas 100% mortality was reached in approximately 11 hr in the shallow tanks (Figure 6).

Observations in the deep tank during tests with the coho and chinook salmon indicated that most fish remained between about 1 and 4 m of the surface. Light intensity and turbidity possibly influenced the depth distribution. During these tests, artificial light at an intensity of about 100 footcandles was present at the surface of the water. Turbidity in the tank was minimal; a Secchi disc was visible at the bottom of the tank and the Jackson turbidity unit measurement was 0.

It is difficult to relate tests in the tank to natural conditions because turbidity in natural water varies greatly. In the Snake River, turbidity as measured by a Secchi disc varies from 0.2 to 8.0 m, depending on season and location. Turbidity usually is high during the spring runoff in both the Snake and Columbia Rivers; readings are seldom over 1 m on the Snake River (Ebel and Koski, 1968). This high turbidity limits visible light penetration to a maximum of about 1.5 m (observation verified by scuba diving). We therefore believe that juveniles as observed in the tank were at greater depths than they might be in the Snake or Columbia Rivers during the spring migration. Durkin, Park, and

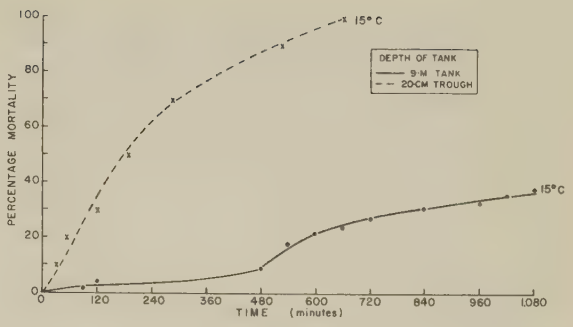

FIGURE 6.—Comparison of LE_{100} curves of wild spring chinook salmon acclimated at 10° C and subjected to a 5° C increase (15° C) in tanks 20 cm and 9 m deep that were supersaturated with nitrogen gas at 130% saturation. Oxygen concentrations varied from 115 to 125% saturation.

Raleigh (1970) found that most juvenile salmon were near the surface as they entered Brownlee Reservoir. Fish in the Columbia and Snake Rivers apparently do not sound to a depth sufficient to compensate for nitrogen saturation levels exceeding 130%; hence the mortalities reported herein are probably on the conservative side. We also emphasize that even though the option of having sufficient depth reduced the mortality rate, substantial mortalities occurred.

TEMPERATURE STANDARDS FOR RIVERS WITH NITROGEN SUPERSATURATION

Our test temperatures and experimental design were purposely selected so that these data could be compared with the results reported by Brett (1952). Brett cautions that the information he presents should not be applied verbatim to other environments. Because of the excellence of his work and the lack of later findings concerning temperature tolerance of Pacific salmon, the upper lethal levels established in his paper are widely quoted and used for setting temperature tolerance standards for rivers and streams containing salmon—without regard to other physical and chemical characteristics of the water. The changes in Brett's tolerance curves caused by the stresses of supersaturation of nitrogen gas were obvious.

Although complete statistical analysis of our data are not presented in this paper, the differences shown between tolerance curves of fish tested in water with and without supersaturation of nitrogen are so great that conclusions concerning the effect of supersaturation can be made with relative confidence.

Substantial mortalities will occur to migrating juvenile salmon and trout in the Columbia and Snake Rivers—even if no thermal plume or increase in temperature is encountered—whenever the populations must pass through large areas where 125 to 130% saturation of nitrogen occurs. Studies of vertical distribution (e.g., Smith, Pugh, and Monan, 1968; Durkin et al., 1970) indicate that the majority of migrants are in surface waters, with substantial numbers in waters less than 2 m deep. This is too shallow to compensate for nitrogen levels as high as 130%. Surveys of nitrogen levels by Ebel (1969), by Beiningen and Ebel (1971), and by NMFS and State fisheries personnel of Washington and Oregon during the 1970 spring migration, verify that nitrogen in large areas of both rivers exceed 130% saturation. Examination of fish in cages suspended on the surface and at various depths revealed that mortalities caused by nitrogen often exceeded 40% in a deep (4.5 m) cage where the fish could sound at their volition. Periodic checks of juveniles in the Snake River by NMFS personnel in 1970 indicated that 25 to 45% of the chinook salmon and 30 to 58% of the steelhead trout migrants arriving at Ice Harbor Dam had external symptoms of gas bubble disease. We made similar observations of migrants at The Dalles and McNary Dams in 1968 and 1969 and recorded similar findings.

Obviously the migrating juvenile salmon and trout in the Columbia and Snake Rivers are under stress during periods of nitrogen supersaturation. Any increase in temperature over the ambient river temperature, then, will harm these populations. Mortalities already occurring will be accelerated even with minimal temperature increases. Our data show that LE_{50} levels of temperature (Figures 1-4) are far higher than could be accepted as standards for upper limits of rivers containing trout and salmon even at normal concentrations of dissolved nitrogen. The time to first mortality of wild spring chinook salmon, for example, that were acclimated to 10° C and tested in supersaturated water at 23° and 25° C was 10 and 3 min, respectively (Table 8). Temperatures and temperature increases such as these occur in thermal effluents (Coutant, 1969), and substantial mortalities could occur to juvenile salmon and trout passing through thermal plumes.

During spring and summer when flows are low, increases in temperature of the Columbia River from Priest Rapids Dam to the forebay of McNary Dam have been as high as 2.5° C (Ebel, 1969). Increases in temperature over the acclimated temperature greatly accelerated time to death of juveniles when supersaturation of nitrogen gas was present in the test water whether the fish were held in shallow or deep tanks. However, during the low flow periods when temperature increases such as this occur, nitrogen saturation levels are usually low and mortalities such as indicated in the tests would not occur.

The obvious results of these tests are that supersaturation of nitrogen must be considered when setting temperature standards and that any increase allowed over the ambient temperature of the river during periods when the river is supersaturated with nitrogen will be detrimental to salmon and trout populations.

CONCLUSIONS

1. Supersaturation of nitrogen drastically affects the tolerance of juvenile coho salmon, chinook salmon, and steelhead trout to temperature increases. Tolerance to increases below 26° C is lowered and mortality rates are accelerated.

2. Acclimation to higher temperatures will enable the three species to tolerate higher temperatures longer when nitrogen supersaturation is a factor; however, 50% mortality will be reached in less than 18 hr at all acclimation temperatures with supersaturation of nitrogen at 125 to 130%. No temperature is suitable at the 125 to 130% level of nitrogen supersaturation.

3. Depth is an important compensating factor

when supersaturation of nitrogen is present. Tests in the deep (9-m) tank, where fish were free to roam from the surface to the bottom, revealed that mortality rates were much lower and tolerance to temperature increases was increased if the juveniles had the option to sound when subjected to temperature increases.

4. Coho were the most tolerant, chinook next, and steelhead the least tolerant to temperature increases when the water was supersaturated with nitrogen. When supersaturation was not a factor, coho and steelhead were about equally tolerant to temperature increases and chinook the least tolerant.

5. Any increase in temperature allowed over the ambient temperature (whether high or low) of the river during periods of supersaturation of nitrogen will be detrimental to migrating juvenile salmon and trout. Temperature standards should account for the effect of supersaturation of nitrogen gas.

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CONTRIBUTION TO THE POPULATION DYNAMICS OF ATLANTIC ALBACORE WITH COMMENTS ON POTENTIAL YIELDS[1]

GRANT L. BEARDSLEY[2]

ABSTRACT

Length-frequency data on Atlantic albacore from the Bay of Biscay surface fishery and the Atlantic longline fishery were analyzed. Lengths at age were estimated and the von Bertalanffy growth parameters were calculated: $K = 0.141$, $L_\infty = 140$ cm, and $t_0 = -1.63$ years. Instantaneous rates were computed on an annual basis. The total instantaneous mortality coefficient was estimated as 0.96 for albacore in the Bay of Biscay fishery and 0.79 in the longline fishery. Analysis of catch and effort data suggested that greater yields are available from the North and South Atlantic longline stocks though stock identification in the South Atlantic is not clear. Estimates of population structure in the North Atlantic were made by utilizing total instantaneous mortality rates of 0.50, 0.96, and 1.40 and an instantaneous natural mortality rate of 0.23. The population based on a total mortality coefficient of 0.96 appeared to be the most reasonable.

The albacore, *Thunnus alalunga*, has become increasingly important to the Atlantic tuna fisheries in recent years. From 1956 to 1961 the Japanese longline fishery in the Atlantic was primarily directed at yellowfin tuna, *T. albacares*, but rapidly declining catch rates for yellowfin soon forced a shift of fishing into primarily albacore areas (Wise, 1968). As a result of decreased yellowfin catches and a corresponding shift in fishing toward albacore, the average number of albacore caught yearly by the Japanese in the Atlantic increased from 228,000 in the years 1956-61 to 1,332,857 in the years 1962-68. The percentage of albacore in the combined catch of albacore and yellowfin in the Atlantic by the Japanese rose from an average of about 18.7% in 1956-61 to 67.7% in 1962-68 (Figure 1).

Since 1965 the Japanese have significantly curtailed their longline fishing in the Atlantic. From a high of almost 100 million hooks in 1965, they set slightly over 30 million hooks in 1967 and again in 1968. This decrease, however, has been offset by the entry of China (Taiwan) and South Korea into the fishery as well as small amounts

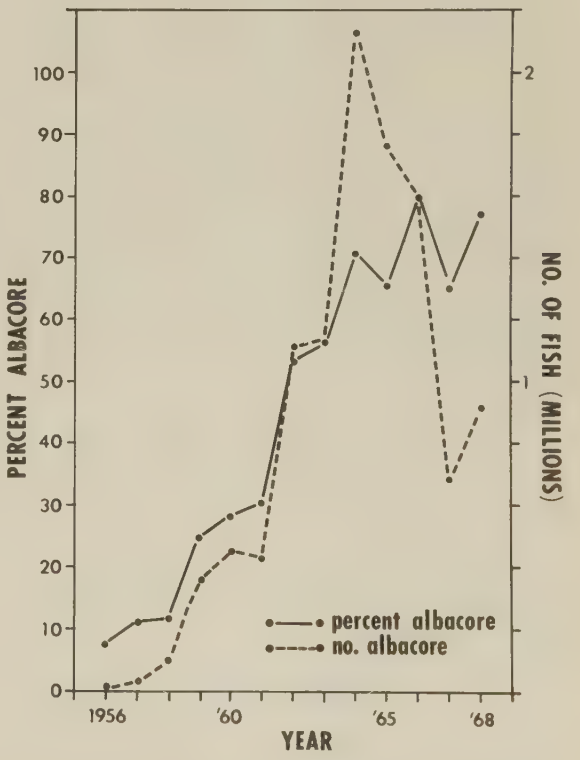

FIGURE 1.—Total number of albacore caught and the percentage of albacore in the combined yearly albacore-yellowfin tuna catch by Japanese longliners in the Atlantic Ocean, 1956 through 1968.

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of fishing by Cuba and Venezuela. In 1968 the combined landings of albacore by China and South Korea were about 15,500 metric tons, which was only 1000 tons less than the Japanese catch for 1968. Recent estimates have placed the Atlantic albacore catch for 1969 by China and South Korea at 19,300 metric tons.

Worldwide demand for tuna is increasing every year, and there is growing concern over the condition and well being of Atlantic tuna stocks. Catch rates of yellowfin tuna in the longline fishery suffered severe declines in the 1960's. Wise (1968), Food and Agriculture Organization (1968), Wise and Fox (1969), Hayasi and Kikawa (1970), and others have examined the problem and have concluded that the longline stocks of yellowfin tuna have been fished beyond their maximum capacity.

This paper is an analysis of some aspects of the population dynamics of Atlantic albacore with comments on potential yields and stock size.

AGE AND GROWTH

There have been few studies on the age and growth of Atlantic albacore. Distinct modes appear in length-frequency distributions of albacore samples from the Bay of Biscay surface fishery, and these modes probably represent age-groups. There is considerable disagreement, however, over the assignment of absolute ages to Atlantic albacore (Table 1).

Le Gall (1949, 1952) worked with length frequencies from the Bay of Biscay. He stated that age-group I was less than 48 cm in length, and that the first group that appeared in the fishery was age-group II (56 cm). Figueras (1957) used vertebrae from 67 fish in his analysis and concluded that 56- to 57-cm albacore were 4 years old and that 17- to 18-cm albacore were 1 year old. Yang (1970) estimated that 56-cm albacore were approximately 3 years old based on results of his analysis of annular markings on scales. Otsu and Uchida (1959b), however, concluded from their study of vertebrae, scales, and other hard parts of Pacific albacore that there were no markings that could be considered age marks.

I used data from the Bay of Biscay for 1967, 1968, 1969, and 1970 (Allain and Aloncle, 1968; Philippe Serene and Jean-Claude Dao, Centre National pour l'Exploitation des Océans, personal communication) (Figure 2) as well as longline data (Figure 3) and estimated lengths at age for Atlantic albacore (Table 1).

Lengths at ages 1, 2, 3, and 4 were estimated by modes in length-frequency histograms from Bay of Biscay samples. The first mode distinguishable in the length frequencies (Figure 2, 1968) is at approximately 44 cm, and I assume that it represents age-group I. There is support in the literature for the assignment of this approximate length to 1-year-old albacore. Otsu and Uchida (1963) indicated that 30- to 35-cm

TABLE 1.—Summary of age and growth investigations on Atlantic albacore.

Investigator	Method	Sample size	Age (years)									
			1	2	3	4	5	6	7	8	9	10
			cm									
Priol (1944)	Scales (total length)	50	50-58	59-74	74-86	86-94	94-98	--	--	--	--	--
Le Gall (1949)	Length frequencies (total length)	--	<25	25-46	46-60	60-74	74-88	--	--	--	--	--
Le Gall (1952)	Length frequencies (total length)	50,000	<48	56	68	81-82	>93	--	--	--	--	--
Figueras (1957)	Vertebrae (total length)	67	17-18	31-32	44-45	56-57	69-70	81-82	91-93	--	--	--
Yang (1970)	Scales (fork length)	159	20.3	39.6	56.1	71.2	80.9	90.3	98.1	--	--	--
Beardsley (present study)	Length frequencies (fork length)	62,602	44	55	64	75	87	95	100	104	108	112

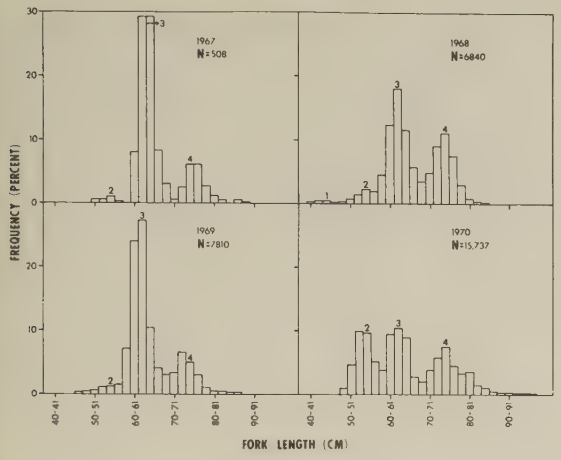

FIGURE 2.—Albacore length-frequency distributions from the Bay of Biscay surface fishery, 1967-70. Estimated ages in years are shown above the histograms.

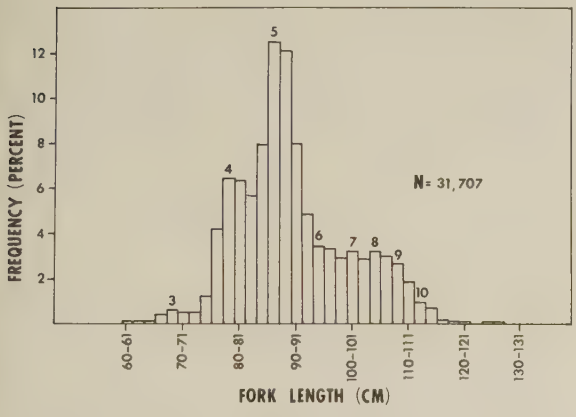

FIGURE 3.—Albacore length-frequency distribution from the Atlantic longline fishery, several years combined. Estimated ages in years are shown above the histograms.

albacore occasionally appear in the Japanese live-bait fishery in spring, and they assume that these fish are approximately 1 year old. On this basis they assign 2, 3, and 4 years of age to 55-, 65-, and 76-cm albacore respectively in the United States west coast fishery. Yoshida (1968) studied age and growth of juvenile albacore based on 35 specimens recovered from stomachs of billfishes in the Pacific. He derived a hatching date of May 1 based on a regression analysis of length of the juveniles against month of capture and concluded that 1-year-old albacore are approximately 38 cm standard length. Although I have assigned a length of 44 cm to age-group I, a more practical approach would probably be to accept Le Gall's (1952) statement that 1-year-old albacore are "less than 48 cm in length."

Longline length frequencies were used to estimate ages 5 and older (Figure 3). The assignment of ages beyond age 5 is somewhat subjective. I assigned ages 7 and 8 to the modes appearing at 100 to 101 and 104 to 105 cm. Other ages were assigned mostly by extrapolation. My estimates agree in most cases with those made for Pacific albacore by Otsu and Uchida (1963). No attempt was made to assign ages beyond age 10 although undoubtedly some albacore in the Atlantic live to be older than 10.

The two modes which correspond to ages 3 and 4 in the longline samples (68-69 and 78-79 cm) are located at a length of 3 to 6 cm greater than the same age in the Bay of Biscay samples. Yang (1970) stated that ring formation on albacore scales occurred in February-March for North Atlantic albacore. The Bay of Biscay samples were taken in summer, and the albacore had completed approximately a half year's growth. Most 3- and 4-year-old albacore captured by longliners are taken in winter when they are first recruited to the fishery. These 3- and 4-year-old fish are at the end of a year's growth or just beginning a new year's growth, and the disparity in the position of the modes between the longline samples and the Bay of Biscay samples represents growth during the period between the summer fishery and the winter fishery.

GROWTH PARAMETERS

I constructed a Walford line (Figure 4) using the lengths at age from this study (Table 1) and took the intercept of the 45° diagonal as an initial trial value for L_∞ in the expression for growth (von Bertalanffy, 1938):

$$\log_e (L_\infty - L_t) = \log_e L_\infty + Kt_0 - Kt.$$

A best fit was obtained with $L_\infty = 140$ cm. K was calculated as 0.141, and t_0 was —1.63 years. Yang (1970) found $L_\infty = 135$ cm and K = 0.19

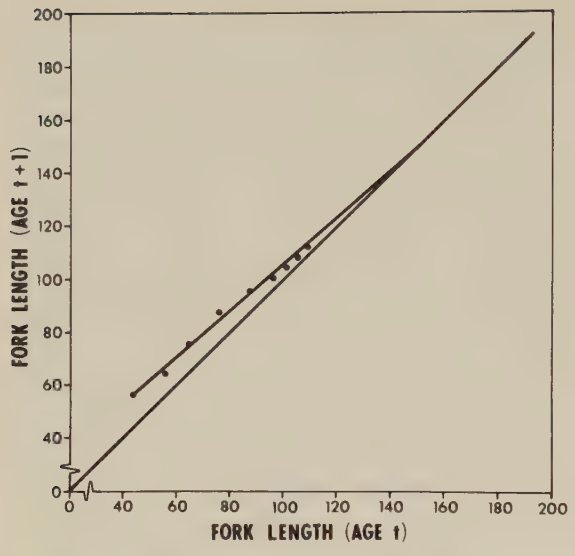

FIGURE 4.—Walford transformation of length in centimeters at age $t + 1$ against length at age t for Atlantic albacore.

from his analysis of albacore growth. The growth curve based on my calculations is shown in Figure 5.

FIGURE 5.—Growth curve for Atlantic albacore.

LENGTH-WEIGHT

De Jaeger (1963), de Jager, Nepgen, and van Wyk (1963), van den Berg and Matthews (1969), and Nepgen (1970) published information on the length-weight relation of Atlantic albacore. All gave separate equations for males and females although de Jaeger (1963) was unable to detect any significant differences in his samples. I combined data from the long-line fishery and the Bay of Biscay fishery and calculated a length-weight equation for both sexes combined since sex information was not available for most of the samples at the smaller sizes:

$$W = 6.303 \times 10^{-6} \times L^{3.28253}.$$

Weight is in kilograms and length is fork length in centimeters (Figure 6).

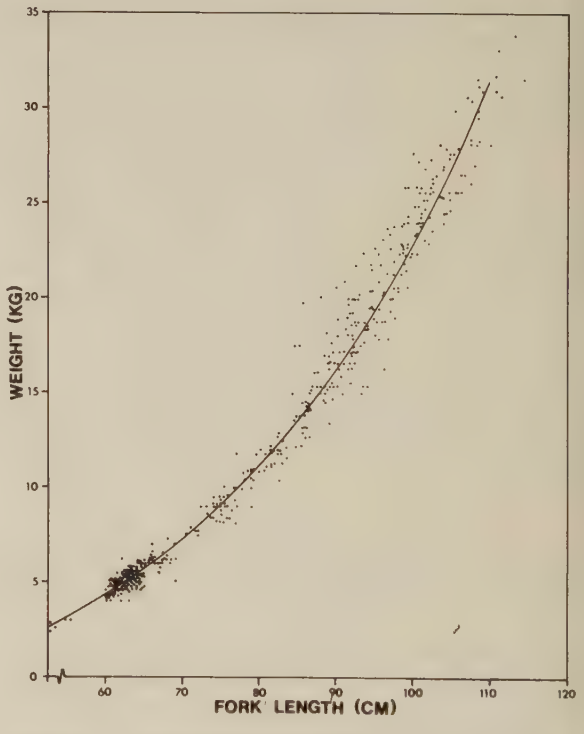

FIGURE 6.—Length-weight relation of Atlantic albacore, both sexes combined.

SEX RATIO

Five hundred ninety-eight albacore were measured and sexed at canneries located in Puerto Rico from December 1969 to September

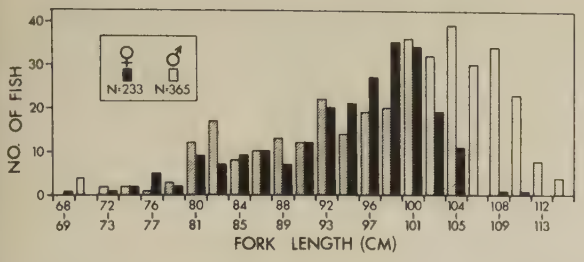

FIGURE 7.—Length-frequency distribution of 598 male and female albacore measured at canneries in Puerto Rico from December 1969 to September 1970. All were caught in the Atlantic by longline gear.

1970. Males constituted 61% of the samples and were more abundant at the larger sizes (Figure 7). Few females appear to attain a length of much over 100 cm. This dominance of males both in numbers and at the larger sizes has been reported for Pacific albacore by Otsu and Uchida (1959a, 1959b) and Otsu and Hansen (1962) and for Atlantic albacore by de Jaeger (1963) and Talbot and Penrith (1963).

MORTALITY

There have been no mortality estimates for Atlantic albacore that I am aware of. Suda (1963) stated that the total instantaneous mortality coefficient of North Pacific albacore is probably around 0.4. He later estimated that the natural mortality coefficient for the same stock is about 0.2 (Suda, 1966). I estimated the total instantaneous mortality coefficient (Z) for Atlantic albacore using Bay of Biscay length frequencies (Figure 2) and longline length frequencies (Figure 3). All mortality rates in the following discussion are instantaneous rates unless specifically designated as annual.

BAY OF BISCAY

If we assume that the 1967, 1968, 1969, and 1970 samples from the Bay of Biscay are reasonably representative of the total catch which is in turn an accurate estimator of the true relative abundance of the different age groups in the fishery, we can calculate a total mortality coefficient from the decline in abundance of a given year class from one year to the next, beginning with the first year it is fully recruited (age 3). This method requires weighting the frequencies by catch per unit of effort (CPUE). Accurate estimates of CPUE for the entire Bay of Biscay fishery are not available, although recent research suggests that a slight decline in CPUE has occurred at selected ports in France in the late 1960's (Jean-Claude Dao, personal communication). I have assumed a constant CPUE over the 4 years in question for the purpose of this analysis since complete figures are not available.

I have also assumed equal recruitment for ages 3 and 4 though this is not likely. Any mortality estimates based on the relative abundance of ages 3 and 4 in the fishery will be affected by relative differences in recruitment. Some 3-year-old albacore and many 4-year-olds are recruited to the winter longline fishery in the North Atlantic; however, for the 4 years, 1965-68, the average number of 4-year-old albacore caught in the North Atlantic winter fishery was only about 40,000. This is a relatively insignificant number when compared with the total number of 4-year-olds available in the Bay of Biscay fishery. It is not known if all the survivors return to the Bay of Biscay the following summer although it is probable that most of them do. If 4-year-old albacore do not all return to the Bay of Biscay from the winter longline grounds then mortalities will be slightly overestimated.

Mortality coefficients were calculated from the decline in abundance from age 3 to age 4 only, and the frequency polygons were divided in the following manner. Where there was an obvious null between age classes, for example at 70 to 71 cm in the 1967 plot, the number of fish in that length group were evenly divided, half were assigned to the age above and half to the age below. Where there was no obvious null, as between ages 2 and 3 in the 1969 plot and between ages 4 and 5 in almost all the plots, the dividing point was placed at a length approximately half way between the assigned lengths at age obtained from

Table 1. Using this method I obtained the following values of Z:

Year class	Z
1964 (3 years old in 1967)	0.73
1965 (3 years old in 1968)	1.04
1966 (3 years old in 1969)	1.12

The average total mortality coefficient over the 3 years was estimated to be 0.96.

LONGLINE FISHERY

A total mortality coefficient was calculated for albacore in the longline fishery using a formula derived by Beverton and Holt (1956):

$$Z = \frac{K\,(L_\infty - \bar{L})}{\bar{L} - L_r}$$

where $\bar{L}$ is the average length of the fish in the catch that are as large as or larger than the first fully recruited length, L_r.

Using: $L_\infty = 140$ cm
$K = 0.141$
$\bar{L} = 94.2$ cm
$L_r = 86$ cm

then:

$$Z = 0.79$$

The total mortality coefficient is not incompatible with the average Bay of Biscay estimate if we consider that the longline is probably relatively inefficient compared with surface gear; hence fishing mortality in the longline fishery and consequently total mortality (assuming natural mortality stays nearly the same throughout the life span of the fish) is probably less than in the surface fishery.

The albacore samples used to estimate mortality in the longline fishery were taken over several years from different areas in the Atlantic. It is very likely, however, that the composite length-frequency distribution in Figure 3 is not a completely accurate picture of the length composition of albacore in the Atlantic. Size distribution in the winter fishery, for example, is entirely different from that in the summer fishery, and suitable samples from each fishery would have to be taken to ensure a representative picture over the entire ocean.

YIELD ESTIMATES

There are five major areas in the Atlantic where longliners concentrate on albacore. I have designated these areas A through E in Figure 8 and for ease of discussion will subsequently refer to these areas by their letter designation. Areas A, B, C, and D were described by Beardsley (1969) and Koto (1969) as major fishing areas. Area E off the coast of Argentina, Uruguay, and southern Brazil has only recently developed into a relatively major albacore fishing area. Of the four areas discussed by Beardsley and Koto, only area C has shown a decline over the years in catch rate (Figure 9). Areas A and D produce fish that are relatively small for longline fish and presumably are recruits to the longline fishery. Recent size data obtained from albacore landed in Puerto Rico and caught in area E reveal that small albacore are also a large part of the catch in this area.

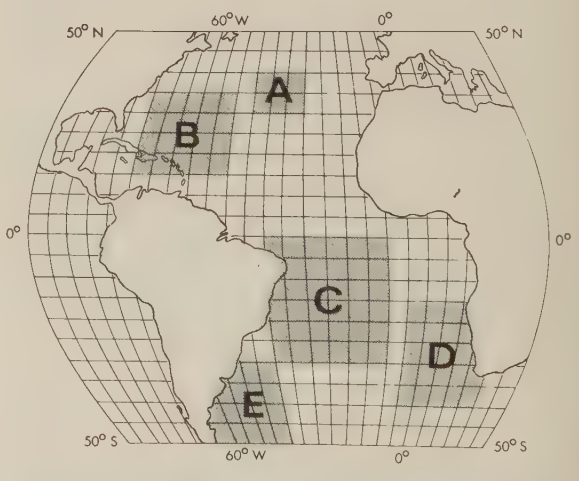

FIGURE 8.—The major longline fishing areas for albacore in the Atlantic Ocean.

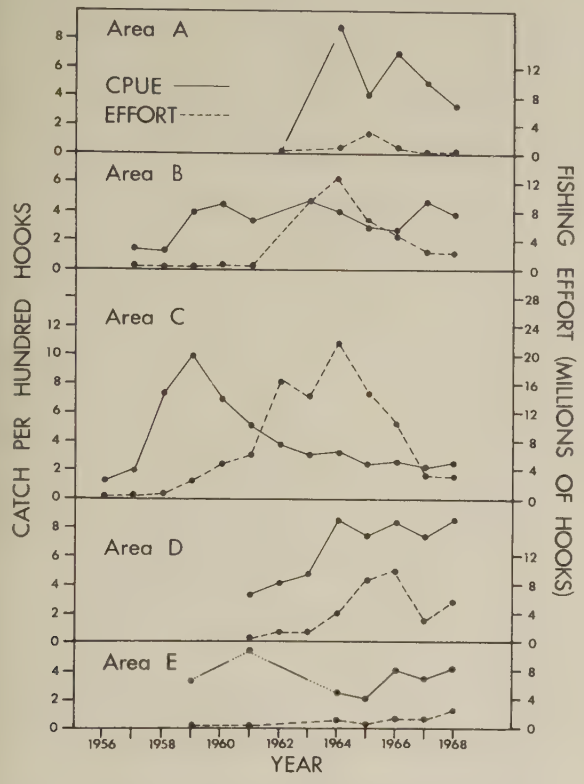

FIGURE 9.—Total longline effort and catch per unit of effort (CPUE) for the five major albacore fishing areas in the Atlantic Ocean, 1956-68.

NORTH ATLANTIC

The North Atlantic supports two different albacore fisheries, the longline fishery and the Bay of Biscay surface fishery, while the South Atlantic has only the longline fishery. The Bay of Biscay fishery, conducted primarily by the French and Spanish, has yielded about 45,000 metric tons annually since 1963. The fishery catches primarily 3- and 4-year-old albacore before they are fully recruited into the longline fishery.

There is evidence that albacore stocks in the North and South Atlantic are separate (Beardsley, 1969; Koto, 1969; Yang, Nose, and Hiyama, 1969). Koto indicates, however, that there may be some mixing of immature albacore between the South Atlantic and Indian Oceans. I combined catch and effort data from the two major albacore fishing areas in the North Atlantic and from the three areas in the South Atlantic and treated each group as separate stocks.

From 1957 through 1965 I used only Japanese data (Shiohama, Myojin, and Sakamoto, 1965; Fisheries Agency of Japan, 1966, 1967a, 1967b) since the longline fishery during those years was almost exclusively Japanese. For 1966, 1967, and 1968 I used Japanese data (Fisheries Agency of Japan, 1968, 1969, 1970) as well as estimated Chinese and Korean catch data (Wise, 1970). Catch per unit of effort (CPUE) in this discussion is the number of albacore caught per hundred hooks fished. CPUE was calculated by summing the number of albacore caught in a given area in a given year, multiplying by 100, and dividing by the number of hooks fished in that area during the year. Only the catch data were available from the Chinese and Korean fishery. Total Chinese and Korean fishing effort for 1966, 1967, and 1968 was obtained by using Chinese and Korean albacore landings and Japanese CPUE and back calculating to the number of hooks fished. This procedure assumes that CPUE for the Chinese and Korean fleets was the same as for the Japanese fleet. This is probably not true; however, the difference is not likely to be large. The Chinese and Korean fishing effort in the Atlantic was not great until 1968 and by then their fishing efficiency was probably comparable to that of the Japanese.

One of the more common mathematical models used to express yield from a stock of fish is the equilibrium-yield model used by Graham (1935), Schaefer (1954, 1957), and others. One of the major advantages of this type of model is that it requires only catch and effort data. Assuming a fishery that has attained equilibrium conditions, a plot of CPUE against effort should show a linear decline which will produce a parabolic curve of yield when plotted against effort. Fox (1970) has argued that the relationship between CPUE and effort is more nearly exponential than linear. Both models, however, predict almost identical yields for the ascending limb of the yield curve. The major difference in the two models occurs after theoretical maximum yields have been exceeded. I chose to limit my analysis to the linear model. The Atlantic longline fishery, however, has never been under equilibrium

conditions. I adjusted for this by using a method suggested by Gulland (1961) whereby effort is an average of the current year's effort (X_i) and the effort from some number of preceding years (X_{i-1}, X_{i-2}, X_{i-3} . . . .), depending on the average number of years a year class is available to the fishery. I used for North Atlantic albacore an average of effort in the current year and the two preceding years:

$$\bar{X} = \frac{X_i + X_{i-1} + X_{i-2}}{3}.$$

The results (Figure 10) show that in the North Atlantic there has been only a slight decline in CPUE over the history of the fishery. When actual catch and effort data are plotted on the predicted yield curve, only in 1964 did yield exceed even 50% of the predicted maximum. It is likely, therefore, that an analysis using an equilibrium-yield model for the North Atlantic albacore longline fishery is not feasible since the population abundance (as represented by CPUE) has apparently not declined sufficiently to effectively describe the dynamics of the stock in relation to fishing. Consequently, maximum sustainable yield from the North Atlantic longline fishery is not estimable at this time. It appears, however, that increased fishing will result in increased yield with no major decline in CPUE.

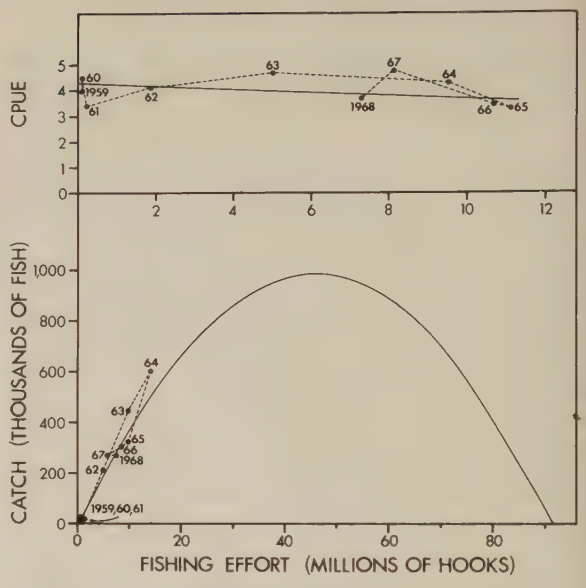

FIGURE 10.—Linear relation between catch per unit of effort (CPUE) and effort (upper panel) and theoretical equilibrium yield curves (lower panel) predicted for the North Atlantic albacore longline fishery. The effort figures in the upper panel are means of the current year's effort and the two preceding year's effort. Effort figures in the lower panel are actual yearly values.

SOUTH ATLANTIC

The albacore longline fishery in the South Atlantic is concentrated in three main areas (Figure 8). During the late 1950's and early 1960's fishing was excellent in area C and fishing effort increased rapidly to a peak of about 22 million hooks in 1964. CPUE declined sharply, however, from a high of 10.0 albacore per hundred hooks, and in recent years has stabilized at about 2.5. In 1961 the Japanese fished in area D for the first time, and this area quickly became the major producer of albacore in the South Atlantic. Fishing is excellent almost year round, and CPUE has remained fairly constant at about 8.0 albacore per hundred hooks over the past 5 years. Area E has recently developed as a good albacore area although effort is still relatively low.

I combined catch and effort data from the Japanese, Chinese, and Korean longline fishery and plotted CPUE against effort in the same manner as for the North Atlantic (Figure 11). The decline in CPUE is more pronounced than for the North Atlantic. The yield curve indicates a theoretical maximum yield of about 1,100,000 albacore from an effort of about 32 million hooks. This yield was equaled in 1964 and surpassed in 1966 and 1968 with an effort of about 25 million hooks.

The South Atlantic albacore fishery has undergone two rather separate and distinct phases. The first phase was from 1956 to 1964 when most fishing effort was in area C. This area produced excellent catches for several years; then catch rates declined rapidly. In 1965 the Japanese increased their fishing in area D in response to excellent catch rates in this area.

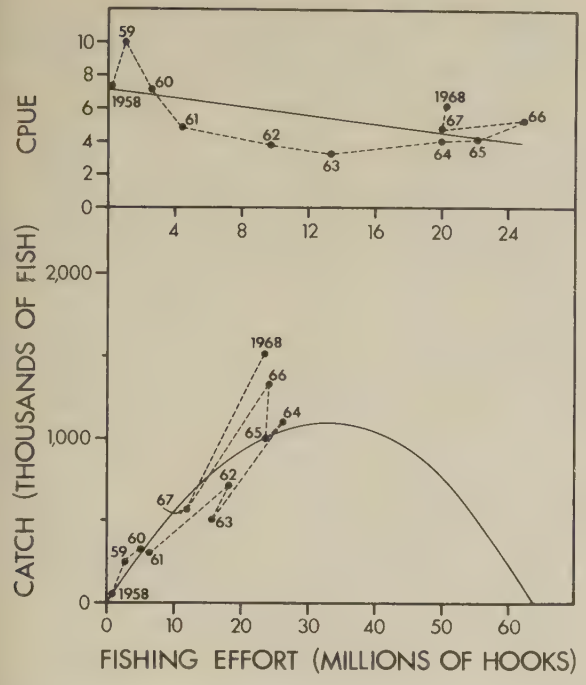

FIGURE 11.—Linear relation between catch per unit of effort (CPUE) and effort (upper panel) and theoretical equilibrium yield curves (lower panel) predicted for the South Atlantic albacore longline fishery. The effort figures in the upper panel are means of the current year's effort and the two preceding year's effort. Effort figures in the lower panel are actual yearly values.

When the data are combined from areas C, D, and E, a decline in CPUE is evident to about 1963 (Figure 11). This decline is primarily in area C. From 1963 to 1968 a steady increase in CPUE is evident which represents the decrease in effort in area C and the increase in effort in area D where excellent catches were being made. It appears from the overall picture of CPUE versus effort that the albacore population in the South Atlantic has declined only slightly in relative abundance as a result of longline fishing.

This may be misleading. I suggested (Beardsley, 1969) that the small albacore in area D formed the recruitment to the South Atlantic population. This hypothesis was based on size differences between the two areas; albacore from area D were small, often averaging as little as 10 to 12 kg, while those caught in area C usually averaged 18 to 20 kg or larger. The monthly distribution of catch rates also indicated seasonal movement between the two areas.

Recent size information obtained from albacore landed in Puerto Rico and caught in area E show that small albacore are a large part of the catch. Recruitment to the South Atlantic population may take place in this area. Koto's suggestion that small albacore move between the Indian and South Atlantic Oceans lends support to this hypothesis. The small albacore in area D may well be transients in the South Atlantic, and any population analysis would have to treat them as a separate stock.

Until the problem of stock identification in the South Atlantic is resolved, any estimates of yield are to be considered tentative. Consistently high CPUE values in area D over the past 5 years suggest that even greater yields are possible from this area. The pronounced decline in CPUE in area C demonstrates a significant response of the population to heavy longline fishing pressure, and any large increase in fishing effort probably would not result in a significant increase in yield.

POPULATION ESTIMATES

I obtained the approximate average number of albacore caught from each age-class in the Bay of Biscay from 1963 through 1968 in the following manner.

Each length-frequency sample from the Bay of Biscay (Figure 2) was separated into age-groups in the same manner as described earlier. The number of albacore in each age-group was then divided by the total number of fish in the respective sample to obtain the percentage contribution of each age-group to the sample. This percentage was considered as being representative of the contribution of that age-group to the total catch for that year. An average percentage contribution over the 4 years, 1967-70, was then calculated for each age-group (Table 2).

I then calculated the total weight of a cohort of 1000 albacore using weights at age (Figure 5) and average percentages obtained above (Table 3). The average annual catch from the Bay of

TABLE 2.—Percentage contribution (in number of fish) of each age-group in the Bay of Biscay from 1967 through 1970.

Age-group	Year				Mean
	1967	1968	1969	1970	
1	00.0	01.1	00.0	00.0	00.3
2	01.9	05.6	03.9	32.5	11.0
3	78.0	54.9	74.6	34.7	60.5
4	16.3	37.5	19.5	24.3	24.4
5	03.8	00.9	02.0	08.5	03.8
					100.0

TABLE 3.—Calculated numbers of fish and corresponding weights for a cohort of 1,000 albacore and estimated average annual catch in number and by age groups from 1963 through 1968 from the Bay of Biscay. See text for explanation of procedures.

Age	Cohort		Estimates for an average year's catch	
	Fish	Weight	Fish	Weight
	no.	*kg*	*no.*	*metric tons*
1	3	5.4	21,327	34.1
2	110	363.0	781,999	2,580.6
3	605	3,267.0	4,300,992	23,225.4
4	244	2,196.0	1,734,615	15,611.5
5	38	554.8	270,145	3,944.1
Total	1,000	6,386.2	7,109,078	45,394.7

Biscay from 1963 through 1968 was 45,400 metric tons (data from Food and Agriculture Organization, 1969). I assumed that the average percentages obtained for 1967 through 1970 were also representative of the years 1963 through 1968.

I used proportion to estimate the average annual catch from the Bay of Biscay in number of fish using the total weight of the cohort, the number in the cohort, and the average annual weight of the Bay of Biscay catch. This total was then separated into age-groups (Table 3) using the percentages in Table 2.

I used these figures to reconstruct three theoretical albacore populations in the North Atlantic based on total mortality coefficients of 0.50, 0.96 (determined from length frequencies), and 1.40 (Tables 4, 5, and 6). In each case I began the calculations using the estimated number of 3-year-old albacore landed. I assumed a natural mortality coefficient (M) of 0.23 and obtained the fishing mortality coefficient (F) by subtraction. I used the number of 3-year-olds landed (L_3), fishing mortality (F), and total mortality

TABLE 4.—Theoretical albacore population in the North Atlantic, ages 1 through 5, based on a total mortality coefficient (Z) of 0.50 from age 3 through 5. See text for procedures.

Age	Number of fish	Z	Total deaths	Natural deaths	Fishing deaths (surface only)
	thousands		— — *thousands of fish* — —		
1	33,372				
		0.23	6,858	6,837	21
2	26,514				
		0.27	6,273	5,491	782
3	20,241				
		0.50	7,965	3,664	4,301
4	12,276				
		0.50	4,831	3,096	1,735
5	7,445				
		0.50	2,930	—	270

TABLE 5.—Theoretical albacore population in the North Atlantic, ages 1 through 5, based on a total mortality coefficient (Z) of 0.96 from age 3 through 5. See text for procedures.

Age	Number of fish	Z	Total deaths	Natural deaths	Fishing deaths (surface only)
	thousands		— — *thousands of fish* — —		
1	15,578				
		0.23	3,201	3,180	21
2	12,377				
		0.30	3,208	2,426	782
3	9,169				
		0.96	5,659	1,358	4,301
4	3,510				
		0.96	2,166	431	1,735
5	1,344				
		0.96	830		270

TABLE 6.—Theoretical albacore population in the North Atlantic, ages 1 through 5, based on a total mortality coefficient (Z) of 1.40 from age 3 through 5. See text for procedures.

Age	Number of fish	Z	Total deaths	Natural deaths	Fishing deaths (surface only)
	thousands		— — *thousands of fish* — —		
1	11,841				
		0.23	2,433	2,412	21
2	9,408				
		0.32	2,577	1,795	782
3	6,831				
		1.40	5,146	845	4,301
4	1,685				
		1.40	1,269		1,735
5	416				
		1.40	313		270

(Z) to determine the number of 3-year olds that died (D_3):

$$D_3 = \frac{L_3 \times Z}{F} .$$

Simple back calculation using the annual mortality rates gave the original number of 3-year-olds present. I was then able to work forward and backward from this figure to obtain estimates at other ages.

Adjustments were necessary, however, in order to obtain reasonable estimates. I used much lower total mortality coefficients for 2-year-olds, for example, than for 3-year-olds. Two-year-olds were not fully recruited, and they constitute only about 10% of the total catch. I also assumed total mortality for 1-year-olds was equal to natural mortality since very few 1-year-olds are captured.

Only one of the total mortality coefficients proved to be completely unreasonable. The estimated number of 4-year-olds present was less than the estimated annual catch of 4-year-olds when $Z = 1.40$, which is obviously an impossible situation. In estimating the other two populations, $Z = 0.96$ appeared to be more reasonable than $Z = 0.50$. When the number of 4-year-old albacore that die of natural causes is obtained by subtracting the estimated fishing deaths from the estimated number of total deaths the result corresponds to an M of 0.20 when $Z = 0.96$, which is close to the assumed natural mortality coefficient of 0.23 (based on Suda's (1966) estimate) estimated for ages 1 through 3. When $Z = 0.50$, the number of natural deaths of 4-year-olds corresponds to an M of 0.32.

If we use the figures in Table 5 and apply a total mortality coefficient of 0.96 from age 5 to age 6 and 0.79 (from longline data) from age 6 through age 10, we can reproduce what theoretically occurs in the North Atlantic longline fishery in an average year. Table 7 shows that the longline fishery should capture about 718,000 albacore, ages 5 through 10, in the North Atlantic each year. The actual average number of albacore captured annually from 1963 through 1968 is estimated at 513,000 (data from Wise, 1970). This difference is large, but a relatively small adjustment in the number of recruits at age 5 would bring the figures closer together. For example, by decreasing the number of recruits to 1,100,000 the potential longline catch was calculated as 533,000 fish, much closer to the 6-year average of 513,000.

TABLE 7.—Theoretical yields from ages 5 through 10 based on the population in table 5 with natural mortality coefficient 0.23, and total mortality coefficient 0.96 from age 5 to age 6 and 0.79 from age 6 to age 10.

Age	Number of fish	Total deaths	Natural deaths	Fishing deaths
		thousands of fish		
5	1,344			
		829	199	360 (longline)
6	515			270 (surface)
		281	82	199
7	234			
		127	37	90
8	107			
		58	17	41
9	49			
		27	8	19
10	22			
		12	3	9
Total	2,271			718 (longline only)

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PLANKTON POPULATIONS AND UPWELLING OFF THE COAST OF PERU, JUNE 1969

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ABSTRACT

Plankton populations associated with upwelling areas and the changes with time of upwelled patches were studied off the coast of Peru near Supe in June 1969. Two patches, detected by their higher nutrient levels, greater chlorophyll pigment concentrations, and lower surface temperatures than surrounding waters, were each monitored for several days, during which time they gradually lost their identity. Actively photosynthesizing phytoplankton crops (doubling time ca. 1.4 days) of predominantly small monads and other flagellates were found in both patches. The zooplankton populations in the patch areas were estimated to be consuming no more than about 25% of the daily phytoplankton production. Direct determination of physical mechanisms affecting the patches showed a relatively high level of vertical instability in Patch 1 which would allow for turbulent mixing and the carrying of phytoplankters below the compensation depth. A horizontal divergence was associated with Patch 2 and would also have the effect of dissipating the patch. Approximate estimates of upwelling suggested vertical velocities of about 2×10^{-2} cm/sec in both patches.

Interest in biological production in Peruvian coastal waters has been high in recent years. The prosperous fish-meal industry developed around the anchovy, *Engraulis ringens*, has stimulated numerous investigations by Peruvian scientists of the food chain leading to this commercially valuable fish (see, for example: Guillén and Izaguirre de Rondan, 1968; Zuta and Guillén, 1970; and various "Informes" of the Instituto del Mar del Perú). In addition, massive upwelling and its associated biological activities along the Peru coast has been of concern to investigators from other countries and has resulted in several international cruises which have added to our knowledge of the pelagic ecology of the area.

The distribution of upwelled water at the surface is often in somewhat discrete "patches," perhaps the result of dynamic physical forces such as currents and/or eddies acting in the area. In March-April 1966, Strickland, Eppley, and Rojas de Mendiola (1969) observed low standing crops of phytoplankton (chlorophyll *a*, <2 μg/liter) in high-nutrient patches (e.g., surface NO_3-N, 20 μg at./liter or higher). In other similarly rich water phytoplankton abundance was high (chlorophyll *a*, 15 μg/liter). Barber et al. (1971) reported the surface water in an area of recent upwelling showed a lack of the "organic conditioning compounds" which may be needed for phytoplankton growth. However, in the nutrient-rich but low-chlorophyll patches examined by Strickland et al. (1969) relatively high growth rates (ca. 0.8 doubling/day averaged over the euphotic zone) were found for the phytoplankton. Similar rates (ca. 0.6 doubling/day) can be calculated from the ^{15}N (nitrate and ammonium) assimilation studies done in this area by Dugdale and co-workers (University of Washington Department of Oceanography, 1970).

A high grazing pressure exerted by the pelagic animal populations was considered by Strickland et al. (1969) as a possible underlying cause for the low standing crops in the nutrient-rich patches with active phytoplankton populations. Ryther et al. (1970) also proposed grazing as an important mechanism for the reduction of the

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phytoplankton stock in a patch of upwelled water they observed continuously for 5 days in April 1966, south of Callao. Both zooplankton and the anchovy must be considered as potentially important direct grazers of the phytoplankton. Rojas de Mendiola et al. (1969) found the stomach contents of anchovies collected in February-March of 1968 in the area of this study (i.e., off Supe) to be predominantly phytoplankton whereas those from the south (Tambo de Mora) were mainly zooplankton remains. At that time the phytoplankton crop off Supe was principally diatoms while diatoms were of much less importance in the phytoplankton populations off Tambo de Mora. Rojas de Mendiola et al. (1969) also reported they had some evidence that adult anchovies may prefer phytoplankton while animal plankters are the choice of juveniles (65-70 mm anchoveta).

In May-June of 1969 the Food Chain Research Group of the Institute of Marine Resources, University of California, in cooperation with the Instituto del Mar del Perú studied various aspects of the physical processes and biological populations associated with upwelling along the Peruvian coast during austral fall. This work was carried out as Leg 7 of the PIQUERO Cruise of the RV *Thomas Washington*. A complete description of these studies is recorded in two "unpublished" data records on file with the University of California, Institute of Marine Resources (1970,[3] 1971[4]). From these studies the coastal current system along Peru was also described (Stevenson, 1971). During PIQUERO Leg 8 the work was extended north to the Equator where the zonal circulation was studied (Stevenson and Taft, 1971). Anchovy studies (abundance, schooling, stomach contents, etc.) were carried out by Villanueva, Jordán, and Burd (1969) on board the Peruvian research vessel *SNP-1* during the first week of PIQUERO 7 in an area south of Callao.

Since neither Strickland et al. (1969) nor Ryther et al. (1970) provided quantitative evidence to support the hypothesis that grazing may be an important means of regulating the phytoplankton crop in these waters, one purpose of our present studies was to determine the abundance of the zooplankton—both microzooplankters (see Beers and Stewart, 1970) and larger forms—and to relate this to observations on phytoplankton abundance, growth rates, and taxonomic composition. In addition, we were interested in the "disappearance" of the patches with time. Evidence is examined for a suggestion that patches may dissipate through physical mechanisms such as horizontal and vertical mixing. The detailed study of physical variables has provided insight into factors affecting biological production in the waters off Peru which would not have been appreciated by the biologist working independently.

MATERIALS AND METHODS

Studies were conducted between 13 and 22 June 1969, in the approximate area bounded by lat 10° and 12° S and long 78° and 79° W off Supe. Extensive "surface" mapping operations at various times throughout this period with underway continuous analysis of inorganic nutrients, phytoplankton pigment fluorescence, and temperature allowed for the detection and surveillance of two patches of upwelled water in this area. Water for the mapping as well as for other "surface" sampling described below was taken with a pump fitted into the ship's hull about 3 m below the sea surface. This unit delivered 10 to 11 liters/min through plastic piping. A series of 57 discrete stations were made during the period of observing the patches for sampling the microzooplankton and macrozooplankton populations, obtaining water for primary production measurements and phytoplankton enumeration, and for determining temperature and salinity profiles. These were taken from various depths in and below the euphotic zone within and outside of the patches.

[3] University of California, Institute of Marine Resources. 1970. Research on the marine food chain; progress report, July 1969 - June 1970. Part III. Data record, Cruise PIQUERO, Leg 7. Section 1. Physical, chemical and production measurements off the coast of Peru, 28 May - 22 June, 1969 aboard the RV THOMAS WASHINGTON. IMR Rep. 70-5. (Unpublished manuscript.)

[4] University of California, Institute of Marine Resources. 1971. Research on the marine food chain; progress report, July 1970 - June 1971. Part III. Data record, Cruise PIQUERO, Leg 7. Section 2. The plankton. IMR Rep. 71-10. (Unpublished manuscript.)

Our purpose was to return to the same patch of water, sampling it on successive days as it "evolved." In general, the temperature and fluorescence of the surface water were used to determine the desired location of sampling after the navigational capabilities of the ship had been used to locate the general area.

Physical measurements, i.e., temperature and salinity, were either by continuous vertical profiles generally from the surface to the bottom, or 500 m, using a STD (Salinity-Temperature-Depth Measuring System, The Bissett-Berman Corp. Model 940)[5] or at the surface (3 m) using a thermo-salinograph (The Bissett-Berman Corp. Model 6600T). Both systems were electronically interfaced to a shipboard IBM 1800 computer.

Vertical profiles of current velocity were made at Stations 99 and 101 using a Hydro Products, Model 502, meter having a precision Savonius rotor to sense current speed and a direction vane coupled with a magnetic compass. The instrument, lowered on the hydrowire, measured the currents for 15 min at each of a series of depths through the upper 200 or 500 m. At each station the current direction and speed were referenced to the deepest observation. The lower practical current threshold is considered to be about 2.5 cm/sec.

Phytoplankton nutrient concentrations (i.e., PO_4, $NO_3 + NO_2$, and SiO_3) in water from the surface pump or taken by water bottles from various depths were determined using an Autoanalyzer and methods described in Strickland and Parsons (1968). A Turner fluorometer with a continuous flow-through cell (Lorenzen, 1966) was used for mapping surface phytoplankton pigment distribution. Vertical profiles of extracted chlorophyll and phaeophytin were done following the procedure of Holm-Hansen et al. (1965).

Levels of primary production through the euphotic zone were measured by the radiocarbonate uptake method at seven stations (see Table 3). Stations 59, 68, 77, and 87 were associated with Patch 1 while Stations 88, 93, and 99 were in the second mass of upwelled water (Patch 2) followed. Water was collected by Van Dorn bottles from depths corresponding to 80, 30, 20, 15, 5, and 1.5% of the surface irradiance at each location. These depths were estimated from Secchi disc depths. Incubation of samples in deck incubators cooled by surface seawater was for 6 (noon to sunset) or 24 hr.

At each site where primary production was measured, water samples were taken for analysis by the inverted microscope method of Utermöhl (1958) of the phytoplankton species composition, numerical abundance, and estimates of biomass (volume and organic carbon). Generally aliquots from the several depths sampled at each site were integrated to provide a composite sample over the euphotic zone, preserved with 5% Formalin (pH 8.2 $\pm$ 0.2), and studied as described in University of California, Institute of Marine Resources (1971, see footnote 4) and Reid, Fuglister, and Jordan (1970).

Unconcentrated samples for study of the ciliate populations were taken along with the phytoplankton as above. In addition, the ciliates of the euphotic zone were studied at eight additional sites where the larger zooplankton abundance was measured and they were also determined in integrated samples from depth intervals, generally 20 to 30 m sampled at 5-m intervals, below the photosynthetic compensation point (1.5% surface irradiance) at 10 stations.

Samples of the microzooplankton populations concentrated on 35-μ mesh cloth after excluding larger material on 202-μ mesh filters were collected from the surface (3 m) using the intake in the ship's hull at most stations where biological sampling was carried out and during certain of the mapping operations. These samples provided material for study of all microzooplankton groups other than the ciliates, many of which are too small to be retained by this size mesh. An unconcentrated pump sample taken for total ciliates is not considered here as there were indications the pump was damaging the non-loricate forms. Methods of analysis of the total microzooplankton and ciliate populations including conversion from a volume estimate to organic carbon are given in Beers and Stewart

[5] The use of trade names is merely to facilitate descriptions; no endorsement is implied.

(1970) and University of California, Institute of Marine Resources (1971, see footnote 4).

Larger zooplankton abundance was studied at 21 sites including the four stations associated with Patch 1 but only at one location, Station 93, where productivity was measured in Patch 2. Samples were taken by vertical tows from approximately 100 m to the surface using paired 0.5 m nets having 103 μ mesh. The volume of water filtered was determined by a flowmeter mounted in the mouth of one of the nets. At some stations wire angles of 10° to 25° developed during the sampling. The numerical abundance and biomass of all developmental stages of the copepod *Calanus chilensis* Brodsky were determined. An estimate of the biomass of the total Formalin-preserved net material divided into fractions of >505 μ and <505 μ was obtained as dry weight and converted to organic carbon by multiplying by 0.40. For the discussion the total material is considered to be zooplankton although there was undoubtedly a small fraction of phytoplankton and detritus associated with the net sample.

RESULTS

UPWELLING PATCHES

Periodic changes in position and configuration of the two patches as determined from surface mapping of phytoplankton pigments is shown in Figures 1 and 2. Patch 1, when detected on 13 June, appeared relatively compact and had a maximum surface pigment (Chl *a* and "phaeopigments") concentration of 6 to 8 μg/liter. Surrounding waters showed 1 to 2 μg/liter. The patch was bounded on the south and west by a well-defined front. Surface temperature and salinity within the patch were 19.5° C and 35.15‰, respectively, while values reached 21.0° C and 35.25‰ on moving out of the patch. The levels of temperature and salinity at the surface of the patch were similar to those found at depths of 35 to 45 m and 50 m, respectively. Surface nitrate and silicate concentrations of 16 and 13 μM, respectively, were found in the patch, dropping abruptly to about 10 and 7 μM on crossing the thermal front bordering the patch. A decline of surface pigment and nutrient levels was observed over the period 13 to 21 June. By June 17 it was apparent that this patch was disappearing and a more extensive mapping operation revealed a clearly defined patch, Patch 2, about 16 miles (25 km) south of Patch 1 (Figure 2). Patch 2 surface parameters included: maximum pigment concentration of 6 μg/liter; temperature, 19.5° C; salinity, 35.15‰; nitrate, 10 μM; and silicate, 13 μM. A distinct front bordered the patch on the west. Somewhat colder water (19.0° C) but with a lower pigment concentration ($\sim$3 μg/liter) was on the eastern side. A transect from east to west across Patch 2 passed through water with temperatures from 19° to 21.5° C. Variations of surface chlorophyll with temperature for Patch 2 are shown diagrammatically in Figure 3. This patch was no longer recognizable by 21 June. Mapping operations late in the cruise period revealed the presence of additional patches in the area but time did not allow for their study.

WATER MOVEMENT IN AND AROUND PATCHES

Calculations of dynamic topography suggested that Patch 1 occurred in a cyclonic eddy of the Peru Coastal Current (Figure 4). Based on the displacement of the chlorophyll pigments at the surface, the patch was being shifted to the west at about 23 cm/sec. Beneath the surface the dynamic computations suggested a poleward flow of about 15 cm/sec at 50 m (Table 1, Stations 54, 59, and 78). Cool surface water of relatively low salinity (35.15‰) was found on the nearshore side of the meander.

The limited data available for calculation of the dynamic topography around the second patch (Patch 2) suggested a northward flow of surface water along the western boundary of the front (Figure 4). Direct measurements with a current meter at Stations 99 and 101 in this patch showed a flow of 18 cm/sec to the ENE at 10 m, a stronger southerly flow of 30 cm/sec at 50 m and little current, i.e., less than 5 cm/sec, below 100 m (Table 2). Beyond the temperature-salinity front on the west of the patch, the velocity of the water was about 5 cm/sec toward the ENE

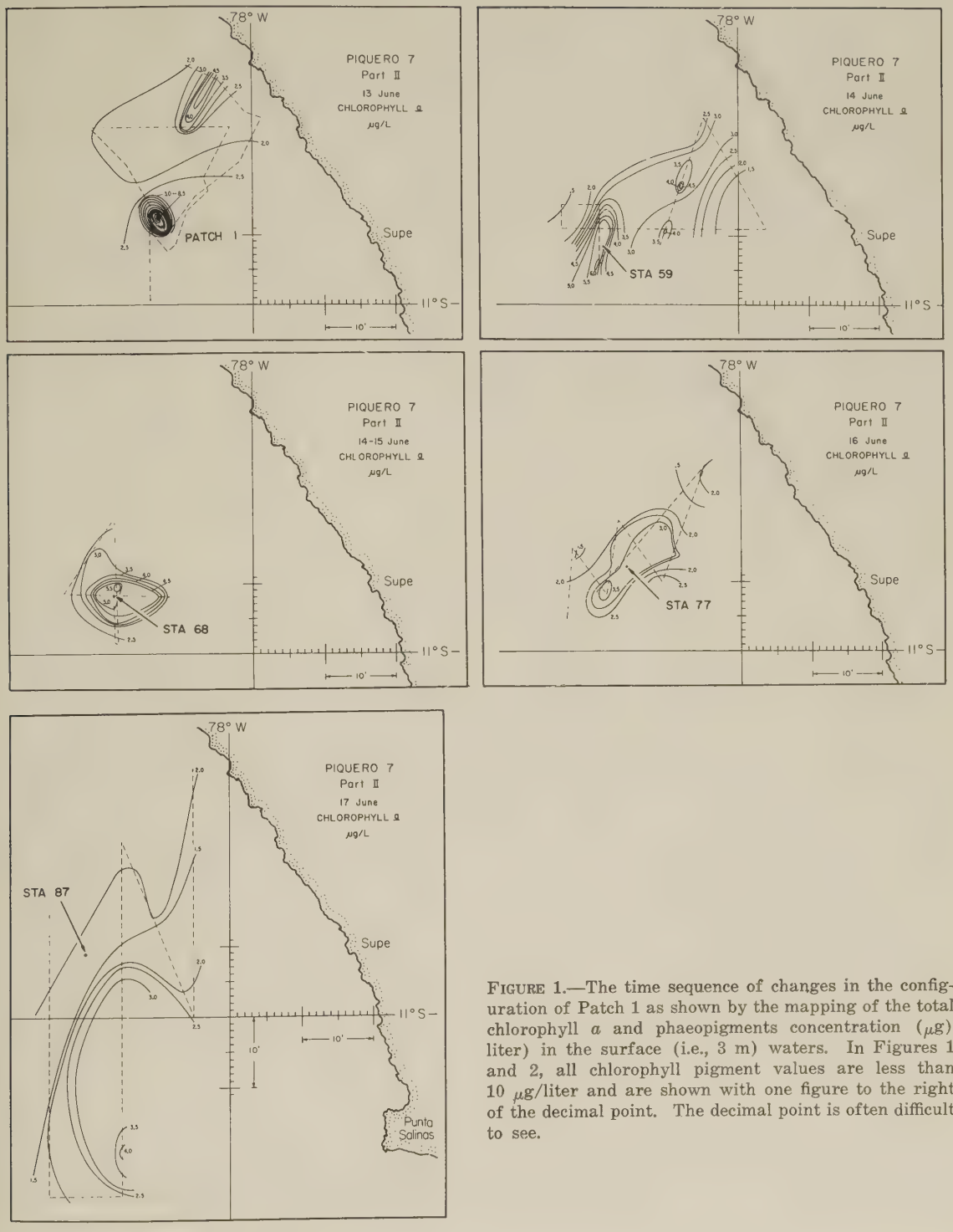

FIGURE 1.—The time sequence of changes in the configuration of Patch 1 as shown by the mapping of the total chlorophyll *a* and phaeopigments concentration (μg) liter) in the surface (i.e., 3 m) waters. In Figures 1 and 2, all chlorophyll pigment values are less than 10 μg/liter and are shown with one figure to the right of the decimal point. The decimal point is often difficult to see.

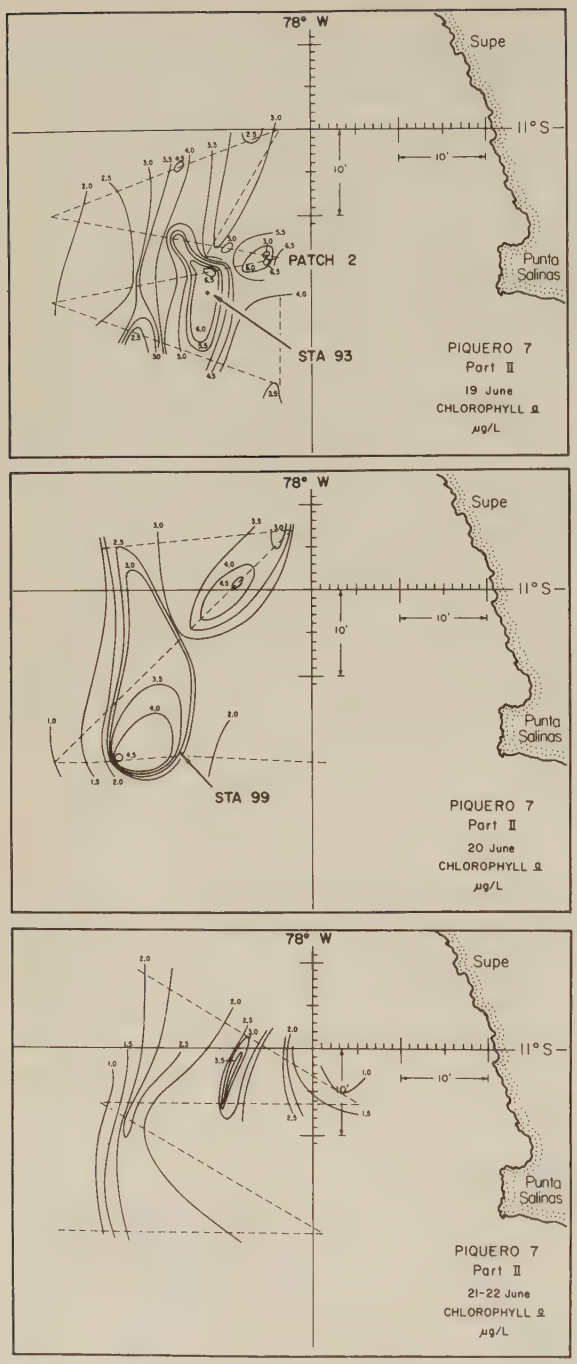

FIGURE 2.—The time sequence of changes in the configuration of Patch 2 as shown by the mapping of the total chlorophyll *a* and phaeopigments concentration (µg/liter) in the surface (i.e., 3 m) waters.

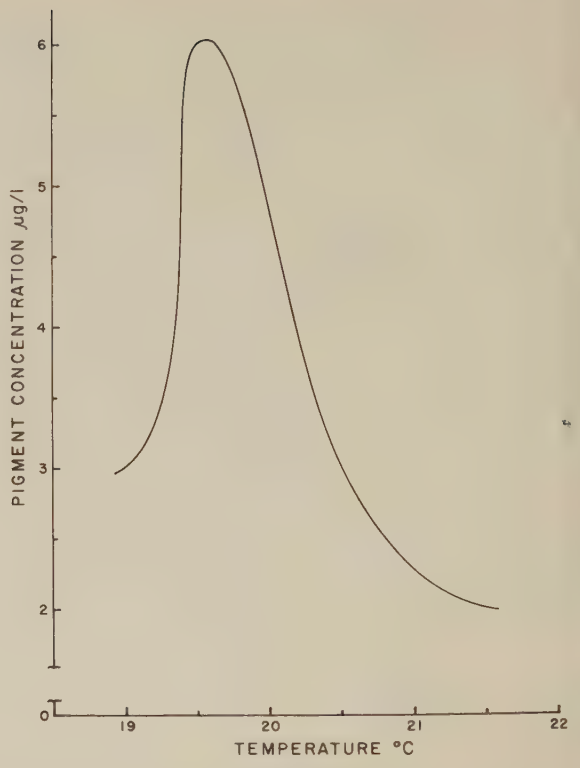

FIGURE 3.—Variation in total chlorophyll *a* and phaeopigments concentration with temperature noted in an east to west transect across Patch 2.

at 10 m (Figure 4). At greater depths at this location flow was generally eastward at velocities up to 4 cm/sec. A small northerly component was seen at 50 m. A horizontal divergence was apparent between the two stations from the zonal components of the velocity measured at 10 m.

In addition to indicating the horizontal direction of water flow, measurements from current meters can be used to estimate vertical shear (Table 2). Shear on the west side of Patch 2 was generally low because of fairly uniform flow toward the east. Maximum vertical shear inside the patch and to the east of the front was up to seven times greater than the maximum to the west of the patch. The large negative meridional (north-south) shear in the patch signified a change from weak northerly flow to strong southerly flow at 49 m.

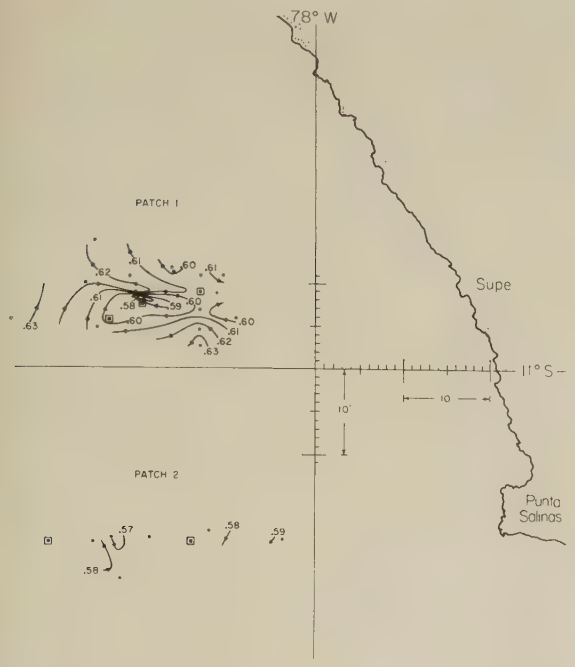

FIGURE 4.—Dynamic topography (in dynamic meters) of the sea surface referenced to the 300 db surface. Patch 1 was observed 13-21 June 1969; Patch 2, 18-21 June 1969. Data from a detailed analysis of stations designated by a square (⊡) are given in Tables 1 and 2.

In order to obtain information on the turbulent activity of the water in the vicinity of each patch, the Väsäilä frequency, N, an indicator of static instability, and the Richardson number, Ri (Phillips, 1966), an indicator of dynamic instability, were calculated at various depths for the three stations in Patch 1 and the two current meter stations associated with Patch 2 (Table 1 and 2). The Väsäilä frequency, based on the vertical density gradient, is often used as an indication of the vertical stability in a water column assuming static conditions, i.e., no vertical shear. Small positive values for N imply the possibility of weak vertical mixing and negative values indicate the probable overturn of the water layer being studied. For the purpose of comparison it was assumed a Väsäilä number less than 1×10^{-3} sec^{-1} signified the start of static instability. Since the effects of a possible vertical shear are not considered, this measure will give an inaccurate estimate of the likelihood of significant turbulence in the presence of nonuniform horizontal currents. The Richardson number, Ri, is generally used to estimate whether turbulent mixing is an important factor for consideration. A Richardson number less than 0.25 is considered indicative of dynamic instability and the development of turbulent mixing. Owing to a lack of current meter data for Patch 1 it was necessary to estimate the shear used for determination of Ri from geostrophic currents.

In Patch 1 conditions of static instability are specifically indicated at a depth of 30 to 50 m for Station 54 (Table 1). The water columns at the other two stations associated with this patch were weakly stable. Dynamic instability was also indicated between 30 and 50 m at Station 54. In addition, the upper 10 m of Station 59 showed dynamic instability. Although static stability was greater at Station 78 than at the other two stations, the water column was dynamically unstable from the surface to 50 m because of the larger vertical shear present.

Conditions in Patch 2 (Table 2) contrasted with those in Patch 1. Vertical shear was generally much less than in Patch 1. This, however, may be partly attributable to differences arising between direct measurements of currents (Patch 2) and estimates of currents based on the horizontal distribution of mass (Patch 1). Compared with Patch 1, the water column in Patch 2 was more stable. The Richardson numbers from the west side of the front on Patch 2 are all very high and indicate conditions that are not favorable for vertical turbulent mixing. In Patch 2 the meridional component of Ri is smaller and suggests that, while the water column is not dynamically unstable in the upper 50 m, turbulent mixing might not subside as quickly as if the water column was highly stratified.

Direct current measurements to the east and west of the front (Patch 2) were made to 200 m and 500 m, respectively. If water motion within the patch at 200 m, however, was similar to the measurements at that depth on the west side of the front, the change in current velocity would be to increase the velocity in the eastward direction by about 4 cm/sec and thereby increase

TABLE 1.—Vertical shear and stability in Patch 1.

Stations	Depth (m)	Väsäilä frequency, ^1N (10^{-3} sec^{-1})	Velocity, ^2V (cm sec^{-1})	Vertical shear, $\frac{\partial v}{\partial z}$ (10^{-3} sec^{-1})	Richardson number,[3] Ri
Station 54	0		−20		
10°51.0′ S		2.5		2.0	1.53
78°13.0′ W	10		−22		
13 June 1969		4.0		3.0	1.74
	20		−25		
		2.5		−1.0	6.10
	30		−24		
		[4]—		−3.5	−1.69
	50		−17		
		12.0		−3.6	10.95
	75		− 8		
		8.3		3.6	5.34
	100		−17		
Station 59	0		18		
10°52.5′ S		2.5		7.0	0.124
78°19.6′ W	10		12		
14 June 1969		5.0		2.0	6.30
	20		10		
		14.0		3.0	21.9
	30		7		
		14.0		6.0	5.08
	50		− 6		
		8.1		8.4	0.921
	75		−28		
		8.3		−1.6	27.0
	100		−24		
Station 78	0		134		
10°54.2′ S		11.0		31.0	0.116
78°23.1′ W	10		103		
16 June 1969		10.0		29.0	0.120
	20		74		
		9.1		37.0	0.060
	30		37		
		13.0		30.0	0.205
	50		−23		
		9.8		7.2	1.85
	75		−40		
		8.3		−5.2	2.56
	100		−27		

[1] The Väsäilä frequency, $N = \left(\frac{g\partial\rho}{\rho\partial z} - \frac{g^2}{c^2}\right)^{1/2}$ (Phillips 1966) where g = acceleration of gravity, ρ = density of sea water, c = velocity of sound, and z = distance below sea surface.

[2] Velocities in this column represent component velocities in the NW-SE direction and are based on geostrophic computations between the individual stations and the adjacent station to the west.

[3] The Richardson number, $Ri = N^2/\left(\frac{\partial v}{\partial z}\right)^2$ (Phillips (1966) where N = Väsäilä frequency and $\frac{\partial v}{\partial z}$ = vertical shear using the component of horizontal velocity, V.

[4] The argument of the Väsäilä equation was negative for this layer and signifies static instability.

the difference in zonal (east-west) velocities across the patch. Water motion in the vicinity of the patch suggests a divergent front with greater eastward water motion found on the nearshore side. The lower surface temperatures and salinity values, relative to offshore salinity, are evidence for localized upwelling and such a mechanism could provide the water needed for replacement owing to horizontal divergence near the surface.

The source for the upwelled water in the two patches we studied appears to be a poleward flow associated with a high-salinity core found at 50 m depth (Stevenson, 1971). Some of the transport from this Coastal Undercurrent is lost through upwelling as the water moves down the coastline. The undercurrent has been traced southward to lat 15°30′ S where it was still present at 50 m. The salinity in the core, however, had decreased to about 35.12‰ and the

TABLE 2.—Vertical shear and stability in Patch 2.

Stations	Depth (m)	Väsäilä frequency, N (10^{-3} sec^{-1})	Velocity (cm sec^{-1}) ^1u	^1v	Vertical shear (10^{-3} sec^{-1}) $\frac{\partial u}{\partial z}$	$\frac{\partial v}{\partial z}$	Richardson number[2] Ri_u	Ri_v
Station 99	10		17	5				
11°20.0′ S		12.2			−0.266	7.69	2,100	2.5
78°14.8′ W	49		18	−25				
20 June 1969		10.9			3.80	−4.20	8.2	6.7
	99		−1	−4				
		5.2			−0.101	−0.404	2,681	168
	198		[3]0	[3]0				
Station 101	10		5	1				
11°20.0′ S		14.3			1.00	−0.250	205	3,280
78°30.0′ W	50		1	2				
20 June 1969		11.8			−0.612	0.408	368	829
	99		4	0				
		5.7			0.200	0.000	822	--
	149		3	0				
		4.6			−0.204	−0.204	514	514
	198		4	1				
		4.2			0.100	0.100	1,950	1,952
	298		3	0				
		4.7			0.150	0.000	995	--
	498		[3]0	[3]0				

[1] Component velocities, u and v, are from current meter measurements and are positive to the east and north, respectively.
[2] Ri_u, Ri_v = Richardson numbers using the east and north velocity components, respectively.
[3] The deepest observations are used for reference and are shown with zero velocity.

measured velocity of about 15 cm/sec was about half that seen in this study around lat 11° S. From the PISCO Cruise of the University of Washington, April-May 1969, Smith et al. (1971) were able to estimate upwelling in a narrow coastal region near lat 15° S. They determined the vertical velocity to average 2×10^{-2} cm/sec over the period of the investigation and estimated it to decrease with increased distance from shore so as to become zero at 20 km offshore.

PHYTOPLANKTON DYNAMICS IN THE PATCHES

Photosynthetic carbon assimilation measurements (Table 3) showed that the phytoplankton crop was physiologically active in both patches throughout the periods of observation even though the patches, as defined by their surface characteristics, were gradually becoming more difficult to recognize (see Figure 5). The decline in the abundance of phytoplankters at the

TABLE 3.—Phytoplankton standing crop as carbon, photosynthetic rate, specific growth rate, chlorophyll *a* and carbon/chlorophyll *a* ratio for plankton patches off Peru, June 1969. (See Table 4 for positions of stations.)

Station	Date	Patch	Euphotic zone depth (m)	Phytoplankton standing crop (g C/m^2)	Photosynthetic rate (g C/m^2/day)	Specific growth rate (μ) (doublings/day)	Chlorophyll *a* (mg/m^2)	Ratio carbon/chl *a* (g/g)
59	14 June 1969	1	18	2.16	1.19	0.64	50.3	42.8
68	15 June 1969	1	28	1.39	0.83	0.68	45.7	30.4
77	16 June 1969	1	30	1.40	1.09	0.83	39	36
87	18 June 1969	1	42	1.91	1.01	0.61	40.8	46.7
88	18 June 1969	2	20	2.56	1.26	0.58	46.8	55
93	19 June 1969	2	27	[1]1.33	1.79	1.23	60.3	22.0
99	20 June 1969	2	30	2.27	1.03	0.54	52.9	42.9

[1] Value probably low, judged from the high μ or low C/chl *a* ratio.

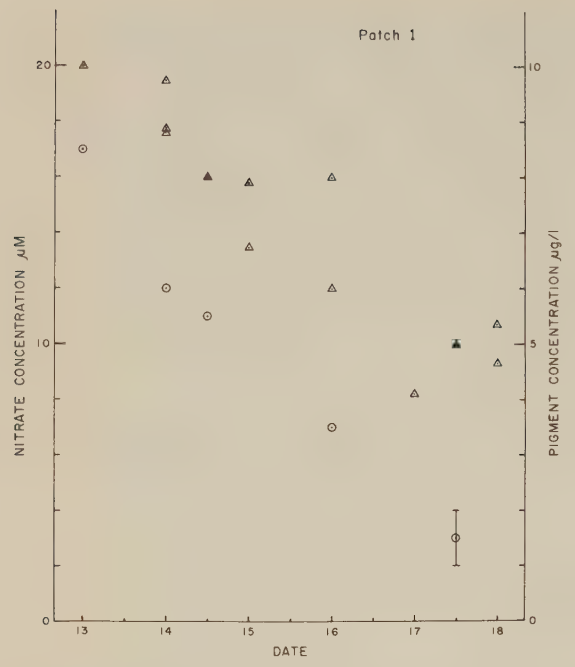

FIGURE 5.—Decline with time in surface nitrate (△) and chlorophyll pigments concentration (⊙) in Patch 1. Solid triangles (▲) are maximum nitrate values found by automatic analysis (Autoanalyzer) during underway mapping. Open triangles (△) are discrete nitrate samples collected on station. Pigment values are maxima of fluorescence found in the mapping area.

surface was compensated for by a deepening of the euphotic zone such that chlorophyll *a*, standing crop as carbon, and photosynthesis showed little variation (<twofold) when integrated over the increasing euphotic zone depth. The specific growth rate, μ, of the crop averaged 0.7 doubling/day over the euphotic zone indicating it should double in 1.4 days if grazers could be eliminated. Similar measurements of μ in March-April 1966 off Peru (Strickland et al., 1969) averaged 0.8 doubling/day for four stations.

The ratio of phytoplankton carbon/chlorophyll *a* (Table 3) averaged 40:1 and was similar to that reported by Lorenzen (1968), using different methods, for a phytoplankton bloom off Peru. The ratio of photosynthetic rate (g C/m^2/day) to chlorophyll *a* (g/m^2) averaged 28 day^{-1}, about one-half that observed by Lorenzen (1968).

As the phytoplankton crop decreased the ratio of phaeopigments to chlorophyll *a* also declined.

SPECIES COMPOSITION OF THE PHYTOPLANKTON CROPS

Taxa with volumes less than that of 10 μ spheres accounted for an average 73% (range: 46%, Station 68 to 93%, Station 59) of the total plant carbon. The dominant forms in both patches were small (2-4 μ and 5-7 μ) cells, often flagellates, and probably cryptomonads or chrysophytes although positive identification was impossible in the Formalin-preserved material. Diatoms never contributed more than 10 to 12% (average pennates + centrics, 5.2%) of the carbon content of the crop. Of the diatoms two species, *Corethron hystrix* and *Nitzschia delicatissima curva*, were the most abundant at all sites. The *Corethron* was one of the very few large taxa that would be retained by phytoplankton nets (35 μ mesh). The "photosynthetic" ciliate, *Mesodinium rubrum* (Taylor, Blackbourn, and Blackbourn, 1969), occurred at all stations but was relatively more abundant in Patch 1 where numbers reached 3000/liter at Station 68. Dinoflagellates contributed 5 to 21% of the total phytoplankton carbon. Unidentified naked forms of cell size <15 μ (equivalent sphere) were the most common of the dinoflagellates. Coccolithophorids (e.g., *Coccolithus huxleyi* and *Syracosphaera quadricornum*) were quite numerous when the patches were disappearing, totaling up to 11 to 14 μg C/liter or 31% (Station 87, Patch 1) and 15% (Station 99, Patch 2) of the plant carbon.

MICROZOOPLANKTON POPULATIONS

Ciliates dominated the microzooplankton populations of the two patches in terms of both numbers and biomass. No marked differences in the abundance of ciliates were noted between the patches. Their standing stock was greatest early in our sampling of each patch (i.e., Station 59, Patch 1; Station 88, Patch 2) owing to relatively large numbers of nonsheathed oligo-

trichs, and was correlated with the generally highest chlorophyll *a* and/or phytoplankton organic carbon level observed. The relatively small number of samples obtained, however, did not allow us to determine the variability within the patch at any given time.

Average ciliate abundance over the euphotic zone at the 15 stations studied ranged from 2400 to 18,000/liter (average, 6200/liter) (Table 4). Oligotrichous forms were at least 75% of the average numbers. Small (10-20 μ) oligotrichs without well-developed sheaths, e.g., *Lohmanniella oviformis*, were generally in much greater number than larger sheathed species, e.g., *Strombidium conicum*. Tintinnid ciliates, of which *Acanthostomella obtusa*, *Craterella urceolata*, *Codonellopsis contracta*, and *Epiplocylis brandti* were common, composed an averaged of 7% of the total numbers. Estimated total ciliate organic carbon levels (Table 4) ranged from 0.7 to 4.8 μg/liter (average, 1.9 μg/liter) of which 17% and 78%, at least, were accounted for by the tintinnids and oligotrichs, respectively.

The abundance of ciliates dropped significantly below the euphotic zone. In the approximately 20-m depth interval beneath the compensation point (10 stations observed, Table 4) ciliate organic carbon was an average 16% of that in the upper waters whereas the average chlorophyll level was still 43% of the average concentration within the euphotic zone. Ciliate abundance over the upper 100 m comparable to the water

TABLE 4.—Ciliate standing stock abundance.

Station	Date	Position	Ciliate standing stock numbers, euphotic zone (no./liter)	Ciliate standing stock biomass, euphotic zone (μg C/liter)	Ciliate standing stock biomass, below (20-m depth interval) euphotic zone (μg C/liter)
[1]59	14 June 1969	10°52.5′ S 78°19.6′ W	10,000	3.3	--
[1]77	16 June 1969	10°48.1′ S 78°16.2′ W	5,300	2.0	0.27
[1]87	18 June 1969	10°51.2′ S 78°20.4′ W	3,800	1.9	--
[1]88	18 June 1969	11°19.5′ S 78°18.6′ W	18,000	4.8	0.25
89	18 June 1969	11°19.8′ S 78°03.6′ W	5,600	1.2	0.16
[1]93	19 June 1969	11°18.8′ S 78°11.8′ W	2,900	0.9	0.38
94	19 June 1969	11°18.8′ S 78°11.8′ W	2,400	0.7	0.38
95	19 June 1969	11°20′ S 78°12′ W	3,800	1.2	0.52
96	20 June 1969	11°20′ S 78°12′ W	4,300	1.0	0.49
97	20 June 1969	11°20′ S 78°12′ W	4,000	1.3	0.43
[1]99	20 June 1969	11°20′ S 78°14.8′ W	6,500	2.0	--
100	20 June 1969	11°20′ S 78°25′ W	11,000	4.0	--
[2]102	21 June 1969	10°55.0′ S 78°24.6′ W	3,300	0.9	0.09
103	21 June 1969	10°54.2′ S 78°19.8′ W	4,700	0.9	--
104	21 June 1969	10°51.2′ S 78°20.4′ W	6,700	2.4	0.31

[1] Stations with primary productivity and phytoplankton crop taxonomic composition data.
[2] Surface chlorophyll *a* level <1.5 μg/liter.

column sampled for the "net" zooplankton was examined at Station 77. Expressed as a percentage of the average ciliate organic carbon concentration within the euphotic zone, the vertical distribution was 30 to 50 m, 14%; 55 to 75 m, 7%; and 80 to 100 m, 6%. Chlorophyll levels over the same depth intervals were 20%, 8%, and 1% of the euphotic zone average. Ciliate organic carbon estimate for the 100-m column was more than 20% of that of the total 103-μ net sample.

The numbers of small shelled sarcodinan protozoa, i.e., Foraminifera and Radiolaria, were relatively low. Numbers counted in the samples integrated over the euphotic zone were too small to provide a good estimate but suggested less than 10 foraminiferans and radiolarians/liter. At the surface, the average abundance of Sarcodina for the 12 stations was low—5.3 organisms/liter or 0.032 μg C/liter.

The metazoan microzooplankters, principally juvenile copepods, were also few in numbers. Less than one metazoan/liter was found, on the average, in +35 sample from the surface. Average numbers in the unconcentrated samples over the euphotic zone were higher (up to 40/liter) but the very few counted puts wide confidence limits on the figure. The size of the "average" individual copepod, both naupliar and post-naupliar, was significantly greater than seen previously (Beers and Stewart, 1970) and this suggests the relative absence, at least at this time of year, of the smaller species and their developmental stages compared with nutrient-rich coastal areas off California.

LARGER (+ 103 μ) ZOOPLANKTON

Standing stock zooplankton at five stations where productivity was measured (Station 59, 68, 77, 87, and 93) averaged 2.4 mgC/m^3 over the upper 100 m and showed less than a twofold difference between sites (Table 5). For the twenty-one 103-μ net samples collected, average zooplankton organic carbon was calculated to be 4.9 mg/m^3. Zooplankters small enough to pass 505 μ mesh were 30% of the total at the "productivity" sites and 25% overall. *Calanus chilensis* (NVI-adults) constituted approximately

TABLE 5.—The standing stock biomass, as dry weight, of the 103 μ net zooplankton samples, 100 m to surface tows.

Station	Date	+103 μ zooplankton dry weight (mg/m^2)		
		<505 μ	>505 μ	Total
58	13-14 June 1969	228	789	1,017
59	14 June 1969	155	273	428
65	15 June 1969	420	933	1,353
66	15 June 1969	384	886	1,270
67	15 June 1969	142	147	289
68	15 June 1969	254	586	840
70	15 June 1969	594	2,410	3,004
73	15 June 1969	433	1,284	1,717
74	16 June 1969	459	1,740	2,199
75	16 June 1969	249	756	1,005
76	16 June 1969	538	1,030	1,568
77	16 June 1969	275	503	778
85	18 June 1969	399	896	1,295
86	18 June 1969	473	911	1,384
87	18 June 1969	83	351	434
93	19 June 1969	130	398	528
95	19 June 1969	145	1,169	1,314
97	20 June 1969	106	685	791

25% of total net organic carbon at the productivity sites. At other stations its estimated abundance as a percentage of the total ranged from <4% to more than 100%. It appeared as though the *Calanus* population associated with Patch 1 was staying with the patch and growing as evidenced by following a cohort of NV and NVI individuals into CI at Day 3 (June 15) and CII at Day 6 (June 18) (see University of California, Institute of Marine Resources, 1971; footnote 4).

DISCUSSION

Many of the specialized studies of biological populations and production in Peruvian coastal waters have been done during the late summer or early fall months of the southern hemisphere, i.e., February to April. The relatively large amount of data available from the Instituto del Mar del Perú provides seasonal coverage of the important food chain variables and allows us to place the conditions we found in this study during austral late fall-early winter in their proper perspective. The transport of nutrient-rich water to the surface through upwelling occurs throughout the year but it is generally most intense in winter (see Wooster and Reid, 1963; Zuta and Guillén, 1970). However, biological production, mainly as evidenced by standing crop

and stock abundance, and primary production levels (Guillén and Izaguirre de Rondan, 1968), appears to be highest during the summer period. Anchovy abundance near the coast is greatest during spring and summer, the time of the most active fishing (Sanchez, 1966).

Strickland et al. (1969) and Ryther et al. (1970) as well as others have pointed out the relatively large variation in upwelled patches at the surface. During the present cruise extensive mapping both to the north and south of Callao failed to show the very high pigment patches (chlorophyll *a*, >10 μg/liter) reported by Strickland et al. (1969) in March-April 1966. Further, the two patches we followed did not have the visually brown coloration described by Strickland et al. (1969) for patches with phytoplankton in bloom conditions. The phytoplankton population of high-chlorophyll, brown-water patches has been found to be principally diatoms whereas the dominant forms in "blue" water areas were generally small flagellates (coccolithophorids and "monads"). In the regions where Rojas de Mendiola et al. (1969) reported the diet of anchovies to be phytoplankton, the crop was principally diatoms and these were the main forms, although not necessarily the same species, recognized in the gut contents of the fish. Even though the cell size of many of the diatom species reported from the brown-water patches is small they are often chain-formers which would provide a size and/or configuration that could be more easily retained on the gill rakers of the anchovy.

The size of most plant cells in the populations found during the present study is relatively small compared with the chain-forming diatoms and, therefore, these may not be efficiently utilized by the anchovy if they pass through their filtering mouthparts. If this size limitation is important, then it is plausible to suggest the anchovy will prey on larger organisms such as many of the zooplankters which in turn have grazed the small algal cells. At the time of year of this study juvenile anchovies (i.e., peladilla) of length 65 to 70 mm and of age 4 to 6 months are generally abundant, having been spawned during the spring and early summer months (see Sanchez, 1966). Rojas de Mendiola (1959)[6] and Rojas de Mendiola et al. (1969) have shown the stomach content of this size class of fish to be mainly zooplankton and have suggested a preference for this food. It would appear this could possibly be due to a lack of the diatoms or other appropriate-sized plant cells. At such times as this when the diatoms are not abundant the food chain leading to the anchovy would necessarily be lengthened by at least one extra trophic level and therefore "efficiency" of utilization of primary production in terms of production of anchovy carbon would be lessened. Growth rate (i.e., increase in length) of anchovies during these winter months is less than half that at other times of the year (Sanchez, 1966). This may be a reflection of the lower abundance of their "food" at this time of year and the need for expending a greater amount of energy to obtain the same or a lesser amount of food.

While some of the diatoms that have been reported in bloom proportions at other times of the year (e.g., Ryther et al., 1970) were present during this study, the absolute abundance of diatoms was low and they were a relatively unimportant component of the total phytoplankton crop. This could be the result of a low rate of production for these forms or may suggest they are being kept down by grazing.

Obvious possible limiting variables of the chemical and physical environment to diatom production do not seem to be relevant here. Even though these observations were made at the winter solstice, light at a location so near the Equator is probably not limiting to production, although at the time of this study the near-coastal region of Peru was often obscured by a persistent cloud cover. And, in fact, photosynthesis was saturated at an irradiance about 20% of that at the surface. Basic nutrient requirements of the diatoms should be met with the levels present. Silicate-Si at four of the five stations where productivity was measured was 8 to 10 μg at./liter or greater through the euphotic zone. Nitrate + nitrite-N levels were

[6] Rojas de Mendiola, B. 1959. Breve informe los hábitos alimenticios de la anchoveta (*Engraulis ringens* Jennys) en los años 1954-1958. A report presented to the Cía. Administradora del Guano, 30 April 1959. (Unpublished manuscript.)

generally in excess of 12 to 15 μM and PO_4-P above 1 μM. It is possible, however, that a nutrient requirement of the diatoms may not be met because of the lack of "conditioning compounds" or some similar mechanism as postulated by Barber et al. (1970). Temperature is of doubtful significance as many of the abundant species in the "blooms" enumerated by Ryther et al. (1970) and Strickland et al. (1969) might be expected to grow equally well at both winter and summer surface temperatures.

Thus, at this time of year the food chain leading to the anchovy probably consists of an intermediate zooplankton step. Villanueva et al. (1969) found stomach contents of anchovies collected 6 to 8 June during this study in an area off Punta San Juan and San Nicholas to be primarily zooplankton. Since no measure of the anchovy standing stock was made, it is not possible to estimate the predation of the anchovy on the zooplankton, but it is possible with our data to evaluate the importance of zooplankton grazing on phytoplankton as a mechanism for preventing their "blooming." The standing stock of zooplankton in the Peruvian coastal waters is generally high (Reid, 1962) although, as pointed out by Gulland (1970), there is probably a marked degree of seasonal and geographical variation in their abundance. Cushing (1969) noted an inverse correlation marked by a short lag between anchovy egg numbers and zooplankton abundance off the Peru coast during the spawning season. He implicated the spawning fish as either the direct or indirect causative agent for this. In either case it was suggested that the low zooplankton stocks and hence their reduced grazing pressure at the end of the spawning season allows for another cycle of biological production. Initially this would be of principally primary production during late summer-early fall followed by an increase in secondary production in the fall. The latter would be available to the juvenile anchovies. While this is simply speculation at the moment, hopefully it will become clearer when more data on the seasonal variation, including small-scale variations, of plankton populations are tabulated (see Gulland, 1970).

A striking feature of the zooplankton populations we observed off Peru was the great absolute and relative abundance of ciliates. The ciliates may be essential elements for the utilization of the small phytoplankton species present, and, if preyed upon in turn by the zooplankton, may represent still an additional trophic level and lengthening of the "food chain" between the primary producers and the harvestable anchovy. The average ciliate organic carbon level over the euphotic zone was about an order of magnitude greater than that found for 12 equidistantly spaced stations from lat 10° N to 12° S along long 105° W in the eastern tropical Pacific (Beers and Stewart, 1971). Ciliate abundance off Peru was similar to the average estimated for a site 1 mile off the coast of La Jolla, Calif., from weekly samples over a 5-month period in the spring and summer of 1967 (Beers and Stewart, 1970). However, off La Jolla the tintinnids accounted for almost three-quarters of the ciliate biomass. Also, just 5 to 6 miles off the California coast the average ciliate abundance (as organic carbon) over the same period had decreased to a level about one-quarter of that recorded for the present set of stations which were generally between 10 and 20 miles off the coast.

Despite their prominence in the zooplankton populations the standing stock of ciliates as organic carbon in the euphotic zone was an average of only 3.2% of the phytoplankton standing crop (6 stations with productivity data). The average daily phytoplankton production over the euphotic zone at these six sites was 49 mg C/m^3. The ciliate carbon was only approximately 5% of the new phytoplankton crop being added daily. An estimate of the fraction of the daily primary production that might be consumed by the ciliates can be made assuming the ciliates require three times their bodily carbon per day. Laboratory culture studies of pelagic ciliates (unpublished) have suggested that tintinnids may be dividing every 1 or 2 days and that the doubling time may be even shorter for the oligotrichs (see also Beers and Stewart, 1970). Values for possible ciliate consumption of new phytoplankton production ranged from 5% (Station 93) to 24% (Station 87), averaging 15%. Other microzooplankton consumption would, on the

average, be a very small addition to the total. If the ciliate populations found off Peru with their dominance of oligotrichous forms receive much of their nutritional requirements through functional chloroplasts in their endoplasm, their direct consumption of phytoplankton would probably be lower than assumed. The gymnostome ciliate, *Mesodinium rubrum*, for which good evidence of endocellular chloroplasts exists (Taylor, Blackbourn, and Blackbourn, 1969) was not included in this calculation.

The *Calanus* standing stocks at the four stations associated with Patch 1 (0-100 m) were estimated to be consuming an average of 22 mg C/m^2/day. These estimates were derived using the data of Mullin and Brooks (1970) on ingestion by the various developmental stages of *Calanus helgolandicus*. The average net primary production over the euphotic zone at these four stations was found to be 1035 mg C/m$_2$/day. Thus the *Calanus* population, which was an average of 27% of the total 103 μ net biomass was consuming only a little more than 2% of the plant production. Even if the remaining 73% of the zooplankton population were migrating to the euphotic zone and consuming phytoplankton at the same rate as *Calanus* the total consumption estimate would still be less than 10% of the daily production. Of course, a significant number of the zooplankters may not be herbivores and also many are much larger forms than *Calanus* and it is probable that their daily ingestion as a percentage of their bodily carbon would be lower than that of *Calanus*. The zooplankton populations below 100 m which might migrate vertically to feed have not been considered here. The majority of tows taken on this cruise were during daylight hours but no significantly greater abundance was evident in the few tows taken during the hours of darkness. The level of dissolved oxygen at 100 m and below in Peruvian coastal waters is low (usually <1 ml/liter). However, Mullin (1966)[7] found numerous zooplankton species inhabiting the oxygen-poor waters off Peru, and some species even showed their greatest abundance at these depths. Nevertheless, in terms of total zooplankton biomass the upper 100 m would probably be of much greater importance than lower depths.

In summary, our estimates call for no greater consumption by the zooplankton than about 25% of the daily primary production. Coupling this with the fact there was no indication that the actively photosynthesizing phytoplankton crop in either patch was increasing with time but, in fact, was actually disappearing, indicates some mechanism other than grazing must be at least partly responsible. Likewise, the fact that there was no significant increase in the phaeophytin level or in the chlorophyll/phaeophytin ratio as the patch was monitored with time argues against zooplankton grazing as a principal cause. Dugdale and Goering (1970) in their study of biological production in the Peru Current during a period of high diatom levels indicated grazing was not the principal source of "loss" of phytoplankton and that the combined anchovy and zooplankton grazing was at a daily level of about 20% of the standing crop. It was further suggested that, of these, the anchovy were a quantitatively more important grazer than the zooplankters.

Strickland et al. (1969) suggested three alternate hypotheses to grazing which implicated physical factors as mechanisms for patch disappearance. In the present study, estimates of vertical shear and stability indicated that turbulent mixing was occurring in the upper 50 m in Patch 1.

Although a lack of current measurements limits our ability to accurately determine local motion within Patch 1, an order of magnitude estimate for the rate of upwelling in the patch is possible from a consideration of the size of the patch and associated biological productivity. From Figure 4 the patch size was found to be 10 km by 5 km by 50 m, in the east-west, north-south and vertical dimensions, respectively. The corresponding volume of the patch is 25×10^{14} cm^3. The patch is assumed to be 50 m thick, below which a subsurface poleward flow is

[7] Mullin, M. M. 1966. Vertical distribution of zooplankton occurring in the oxygen minimum layer off Peru. *In* University of California, Institute of Marine Resources, Research on the marine food chain, Progress report, January 1966 - December 1966, p. 359-369. (Unpublished manuscript.)

present. If the doubling rate for plankton is 1.4 days, then to maintain a constant concentration level requires that the water in the patch is removed at a rate of 2.1×10^{10} cm^3/sec. The southward transport of the undercurrent beneath the patch is estimated at 20.2×10^{10} cm^3/sec, or about 10 times the flow required for replacement of water in the patch. Upwelled water is required to replace the water being removed along the outer boundary of the patch. Since we assume that most, if not all of the water used to replace water lost from the patch, passes through the bottom of the patch at 50 m, the ascending velocity of water at 50 m is estimated to be 4.1×10^{-2} cm/sec for the patch. This is probably an upper limit since other processes also act to reduce the biomass. Unfortunately, only one sub-euphotic zone sample (30-50 m) from Patch 1 is available, and it shows a chlorophyll level only 20% of the average in the upper layer. However, if the ciliate and other zooplankton populations were grazing this material in which no new organic carbon was being produced, it would only be a relatively short time before a marked diminution of the chlorophyll level would be expected. In addition, chlorophyll levels above and below the compensation depth may not be a comparable index to phytoplankton abundance as there is an apparent decrease in chlorophyll level in many phytoplankters when kept in the dark for any period of time. Thus, the plant cell population in the sub-euphotic waters may be underestimated. The phytoplankton cells near to the compensation depth had a lower photosynthetic rate, g C/g Chl *a*/hour (University of California, Institute of Marine Resources, 1970, see footnote 3), than those higher in the water column. Eppley, Holmes, and Strickland (1967) showed that cells in such a physiological state sink at a more rapid rate than faster growing phytoplankters. While sinking or upwelling alone may not result in moving material out of the euphotic zone and preventing a "bloom" from developing, this combined with the turbulence may be a significant contributing factor. Dugdale and Goering (1970) following a high chlorophyll patch of water over 5 days, concluded that approximately 85% of the phytoplankton production at that time was being lost through sinking and mixing processes. At one site examined more closely, 16% of the standing crop was lost daily.

Continued upwelling with the consequent spreading out and/or sinking of the surface waters is another mechanism which would result in masking any bloom that might have developed had the upwelled water mass remained more localized. This was suggested as a means of "preventing" blooms in regions of divergences in the Antarctic (Beklemishev, 1958). Horizontal divergence of Patch 2 with a relatively greater eastward water motion of the nearshore side was indicated by our current measurements. Water on the nearshore side would appear to "stretch" in the horizontal plane and be supplemented by ascending subsurface water. Examination of the graphic reconstruction of chlorophyll distribution (Figures 1 and 2) suggests a spreading out of the chlorophyll patches, becoming diluted in the surrounding area with time. Since dynamic vertical mixing is not indicated by the Richardson numbers for Patch 2, the decrease in chlorophyll may be largely attributed to the divergence and associated upwelling. Horizontal mixing, however, is undoubtedly an important dispersing mechanism in both patches. A rough estimate of upwelling based on the horizontal divergence was made by using the current measurements from Patch 2. Upwelling in the patch is assumed to be confined to a surface layer 50 m thick, where the vertical velocity is a maximum at 50 m (the same depth as the poleward flow of the coastal undercurrent). The resulting estimate of vertical velocity at 50 m is 2.5×10^{-2} cm/sec and compares favorably with the upwelling rate computed with greater accuracy for a nearby coastal zone (Smith et al., 1971). The surface concentration of nitrate declined in the patches over time as did the total chlorophyll pigments concentration (Patch 1, Figure 5). Nitrate consumption by the phytoplankton was calculated, assuming 1 g nitrate assimilated per 6 g of carbon fixed in photosynthesis, and the indicated plant consumption was only about one-third of the observed nitrate decline. This observation again suggests mixing of water in the patches with surrounding less rich water.

We are left with a system that is undoubtedly the result of a combination of interacting factors —both biological and physical—which can be sorted out only semiquantitatively. Apparently a loss equivalent to about 25% of the phytoplankton production may have been due to grazing by zooplankters. As measured here, diffusive mixing of the patches with adjacent waters and sinking of the phytoplankton would account for considerable additional loss of phytoplankton material. In addition other avenues of possible loss such as the direct consumption by the anchovies exist but were not evaluated here. That the relative significance of the different variables may change on a very small scale in time and location at this time of year can be suggested. Such complexity would lead to the variety of conditions that have been described from the coast of Peru.

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NOTES

OBSERVATIONS ON TWO SPECIES OF DOLPHIN (*Coryphaena*) FROM THE TROPICAL MID-ATLANTIC

Large numbers of adult dolphin, *Coryphaena hippurus* Linnaeus, aggregated at night around the U.S. Coast and Geodetic Survey Ship *Discoverer* as it drifted in the tropical mid-Atlantic Ocean in February 1969 (see Stoner, 1969). Only juveniles of *Coryphaena equiselis* Linnaeus, however, were caught under the night light. This note presents additional details of coloration and meristic counts of juvenile *C. equiselis* and reports on mid-oceanic concentrations of adult *C. hippurus*.

The drift track of the RV *Discoverer* on the Atlantic Trade Wind Expedition (ATEX)—lat 13°48′ N long 39°03′ W to lat 09°55′ N long 44° 35′ W, February 5 to 22, 1969—is shown in Figure 1 (see also Potthoff, 1969). The surface temperature of the water during the drift period ranged from 25.3° C to 26.8° C and the water depth from 1,757 fm to 2,753 fm.

Gibbs and Collette (1959) reported that very small juvenile *C. hippurus* resembled miniature feathers with dark and light bars alternating along their bodies and dorsal and anal fins. Very small *C. equiselis*, in contrast, tended to be uniformly dark along their sides, sometimes displaying weak bars along their fins. During the drift, 78 juvenile dolphin were caught by dip net; all were identified as *C. equiselis* on the basis of pigmentation on the caudal and pelvic fins (Gibbs and Collette, 1959) and vertebral counts (Collette et al., 1969). In the present sample, specimens ranging from 25 mm SL to 90 mm SL all had dark vertical bars on their bodies; the bars were most pronounced over the anal fin on the ventral half of the fish (Figure 2). The smallest *C. equiselis* juveniles (less than 25 mm SL) tended to be darker, with less pronounced

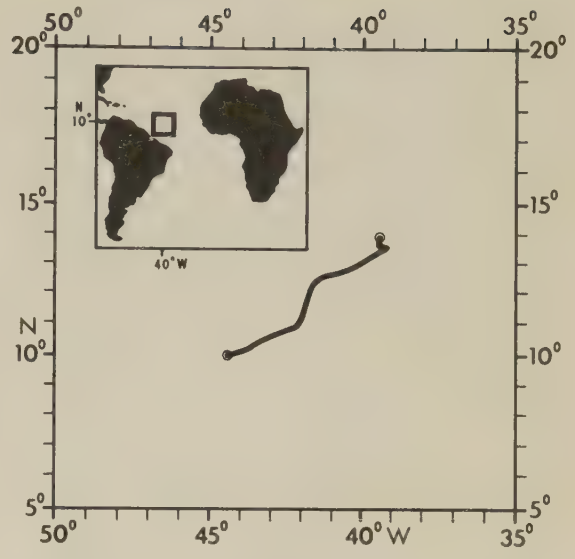

FIGURE 1.—Drift track of the RV *Discoverer* during the Atlantic Trade Wind Expedition (ATEX). The square on the insert map represents the area covered by the map.

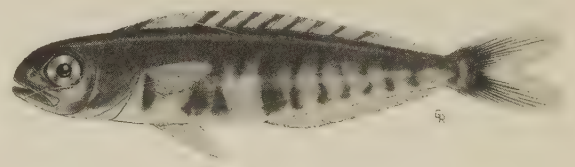

FIGURE 2.—*Coryphaena equiselis*, 40 mm SL from the tropical mid-Atlantic Ocean, caught aboard the RV *Discoverer*, 19 February 1969.

bars or no bars on the body, and specimens larger than 90 mm SL had no bars on their bodies. A single specimen of 230 mm SL exhibited no juvenile coloration. The caudal fork margin was dark, as were the pelvic fins; however, the vertebral count (14 + 19 = 33) was that of *C. equiselis* not *C. hippurus* (Collette et al., 1969). Sixty-three of the juvenile specimens were cleared and stained to obtain vertebral counts (Table 1), leading to their positive identification as *C. equiselis*. In counting

[1] Contribution No. 194, National Marine Fisheries Service, Tropical Atlantic Biological Laboratory, Miami, Fla. 33149.

vertebrae, any vertebra associated with a pair of pleural ribs was counted as precaudal, any vertebra lacking pleural ribs was counted as caudal.

In the cleared and stained juveniles, the modal group of dorsal-fin elements was 55 to 57 (Table 1), which is more similar to the modal group of 56 to 60 for Atlantic *C. hippurus* (Gibbs and Collette, 1959) and of Pacific *C. hippurus* (Rothschild, 1964), than to that of *C. equiselis* (51-55) which these authors reported. The higher mode in these specimens of *C. equiselis* from the tropical mid-Atlantic may be representative of an oceanic population, different from that sampled by Gibbs and Collette (1959) who may have included specimens from more than one population. On the other hand, I may have counted elements in the cleared and stained specimens that were not visible to Gibbs and Collette (1959) in their untreated specimens.

Counts of the anal-fin elements of the specimens from the tropical mid-Atlantic (Table 1) were not appreciably different from those reported by Gibbs and Collette (1959). However, the mode was one fin ray higher than those from the Pacific reported by Rothschild (1964). Total gill raker counts (Table 1) of my specimens were not appreciably different from those reported by Gibbs and Collette (1959) for young *C. equiselis*, but differed from Rothschild's (1964) total counts on adult specimens by two or three rakers. My gill raker counts were made on cleared and stained juvenile specimens and did not include tooth patches on the epibranchial and hypobranchial bones; the gill raker in the epi-ceratobranchial angle was included in the ceratobranchial count. Total counts tended to decrease as fish size increased, which led me to believe that the rakers over the epibranchial and hypobranchial bones are gradually transformed into tooth patches. In specimens below 30 mm SL, the gill rakers over the epibranchial and hypobranchial bones were very small with many minute teeth. In intermediate-sized specimens (40-60 mm SL) some tooth patches could be counted over the two bones along with gill rakers. The epibranchial and hypobranchial bones of juveniles above 80 mm SL were all covered with fine teeth; the hypobranchial bone had no gill rakers associated with it, whereas the epibranchial usually had one gill raker.

Size distribution of juvenile *C. equiselis* caught during the drift period is shown in Figure 3. The mode is from 40 to 44 mm SL. From size

TABLE 1.—Frequency distribution of some meristic characters of juvenile *Coryphaena equiselis* from the tropical mid-Atlantic and data on juvenile and adult *C. equiselis* from Gibbs and Collette (1959) and Collette et al. (1969).

	Fins																										
	Dorsal fin rays																		Anal fin rays								
	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	N	$\bar{x}$	23	24	25	26	27	28	29	N	$\bar{x}$
Tropical mid-Atlantic	--	--	--	--	--	--	2	1	9	15	13	15	6	2	--	63	55.8	--	1	6	23	21	12	--	63	26.6
Gibbs and Collette (1959)	1	--	4	10	15	26	31	40	35	22	9	1	--	--	1	195	52.6	5	24	62	86	38	6	1	222	25.7

	Vertebrae						
	Precaudal		Caudal			Total	
	13	14	19	20	21	33	34
Tropical mid-Atlantic	55	8	8	55	--	63	--
Collette et al. (1969)	67	12	12	66	1	78	1

	Gill rakers											
	Epibranchial		Ceratobranchial			Hypobranchial			Total			
Tropical mid-Atlantic SL (*mm*)	1	2	9	10	11	0	1	2	11	12	13	14
<30	3	12	1	12	2	--	11	4	--	3	7	5
30-50	13	19	1	28	3	5	23	4	2	13	13	4
51-80	8	4	1	11	--	6	6	--	5	4	3	--
>80	3	--	--	1	2	2	1	--	--	3	--	--

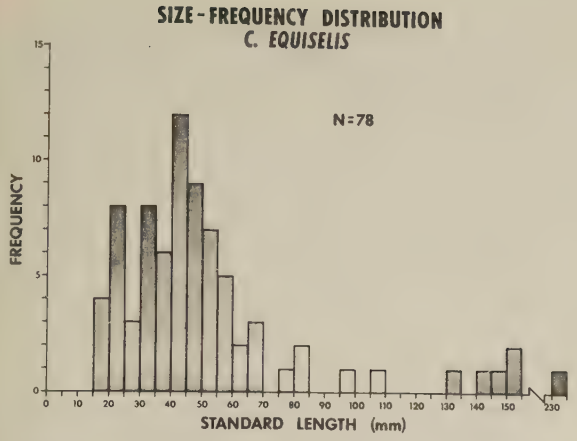

FIGURE 3.—Size-frequency distribution of *Coryphaena equiselis* which were attracted to the night light and caught in dip net during ATEX aboard the RV *Discoverer*, February 1969.

data, I infer that the species spawns in the tropical mid-Atlantic during January and February.

My specimens are presently stored at the Tropical Atlantic Biological Laboratory, Miami, Fla.

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RESPIRATORY, BEHAVIORIAL, AND ENDOCRINE RESPONSES OF A TELEOST TO A RESTRICTED ENVIRONMENT

It is common practice when measuring fish respiration or activity to allow a varying length of time for the fish to become accustomed to the restrictions imposed by the apparatus and to allow time for any oxygen debt to be repaid (Fry, 1957). The following observations indicate that such a procedure may introduce complications in the interpretation of results since the acclimation process results in changes in respiration, behavior, and endocrine activity.

Poecilia reticulata males were placed in groups of 10 in the 100-ml chamber of a continuous flow respirometer. Animals were maintained at 25° C with a 12-hr daylength and fed daily at the start of the light period. Measurements of oxygen were made with the wide bore dropping mercury electrode (Briggs, Dyke, and Knowles, 1958) or by the micro Winkler method (Fox and Wingfield, 1938).

A daily cycle of routine respiratory activity in such an apparatus has already been described (Sage, 1968). The minimum of oxygen consumption occurs at the end of the dark period 23 hr after the last feed and this rate approximates to the standard metabolic rate. Measurement of this rate at daily intervals indicates a progressive fall in standard oxygen consumption (Table 1). A similar fall in respiratory rate

TABLE 1.—Effect of number of days in respirometer on standard rate of oxygen consumption of a group of 10 fish.

Days	Oxygen uptake $mm^3/g/hr$
1	212
2	156
3	126
4	109

to a base line of approximately 100 $mm^3/g/hr$ was observed with four other groups of fish whereas control animals from large containers

maintained a standard respiratory rate of approximately 200 $mm^3/g/hr$.

On removing these fish from the apparatus, their behavior was seen to be very different from control animals kept in 30-liter aquaria and similar to the previously described behavior of fish treated with thyroxine (Sage, 1968). Thus all fish jumped during a 15-min period after transfer from the respirometer to a 50 × 25 cm aquarium with a depth of 2.5 cm of water while only 17% of control animals jumped (Table 2). Similarly all fish kept for 7 days in 500-ml containers and fed ad libitum jumped when transferred to shallow water. The response was therefore to the restricted containers and not to the abnormal once-per-day feeding regime imposed in the respirometer.

TABLE 2.—Effect of maintenance conditions or thyroxine on frequency of jumping.

Treatment	Percentage jumping (number of individuals)
4 days in 100-ml respirometer	100 (30)
7 days in 500-ml container	100 (30)
28 days with thyroxine (1 in 2 × 10^6) in 30-liter container (Sage, 1968)	37 (28)
Control fish in 30-liter container	17 (28)

Sections through the proximal pars distalis showed a degranulation of the TSH cells in the pituitary glands of both groups of fish that had been kept in restricted environments. This was not seen in control animals. Stimulation of the thyroid gland is thus a probable cause of the observed changes in behavior and may also account for the respiratory changes. A fall in standard respiratory rate has been previously observed and attributed to progressive starvation (Fry, 1957). This cannot explain the present results since all respiratory measurements were made an equal time after a feed.

The responses reported here were obtained with container to fish volume ratios of 100 and 500:1. These are larger than the chambers used in most fish respiration studies. Thus Geyer and Mann (1939) suggested a ratio of at least 10:1 for *Perca*.

The present observations indicate that acclimating fish to a restricting apparatus may stimulate the TSH cells and thyroid and produce changes in behavior and respiration. This may be particularly confusing where seasonal changes are being investigated since thyroxine has been implicated in processes of acclimation (Hoar, 1959) and seasonal changes in fish thyroid activity are widespread (Matty, 1960; Swift, 1960) and may be related to seasonal changes in respiratory rate (Fisher, 1958).

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OCCURRENCE OF THE BARRACUDINA, *Paralepis atlantica* KRØYER, IN THE CENTRAL NORTH PACIFIC OCEAN

The barracudina, *Paralepis atlantica* Krøyer, is a bathypelagic fish that has rarely been taken by fishing gear in the North Pacific Ocean; most specimens have been recorded from waters off California in the stomach contents of predators such as whales, fur seals, and scombroid fishes (Rofen, 1966; Kajimura, 1969). Kajimura (1969) extended the known range northward on the eastern Pacific to the Washington coast (lat 46°35′ N, long 124°58′ W) with a specimen taken from the stomach of a northern fur seal, *Callorhinus ursinus*. Maruyama (1958) and Ueno and Abe (1964) reported on three specimens taken by gill net and trawl from the western Pacific Ocean near Hokkaido, Japan (between lat 42° and 43° N and near long 144° E).

The specimen reported here extends the known range of the species northward and to the central Pacific Ocean (lat 48°00′ N, long 165° 00′ W). It was captured on 6 May 1969 in surface waters of 4.5° C with a gill net fished by the RV *George B. Kelez* of the National Marine Fisheries Service. Meristic characters for the specimen are given in Table 1 with ranges for the species as reported by Rofen (1966).

The specimen was torn in half when it was removed from the gill net, preventing accurate measurements; its estimated standard length was 420 mm. It is deposited in the collection of fishes (Catalog no. 20569) at the University of Washington, Seattle.

TABLE 1.—Meristic characters of the specimen compared with those given by Rofen (1966).

Meristic characters	Specimen	Range for species
Fin rays		
Dorsal	9	9-11
Anal	23	20-26
Pectoral	16	15-17
Gill rakers		
Above angle	10	7-10
Below angle	29	25-31
Vertebrae		
Total	61	60-73
Prehaemal	35	28-38

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